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Microscopic analysis of the developing dentition in the pouch young of the extinct marsupial *Thylacinus cynocephalus*, with an assessment of other developmental stages and eruption

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Abstract

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A pouch young of the extinct dasyuromorphian marsupial *Thylacinus cynocephalus* was examined histologically to study the stages of the developing dentition during the pre-eruptive period of development. Both deciduous and successional stages of tooth development were examined, and these were compared to later stages of development and eruption of the teeth in *Thylacinus* and with selected developmental stages of other dasyuromorphians. Our analysis shows that the development and eruption of teeth in *Thylacinus* is most similar to that of dasyurids with only two premolars, such as *Dasyurus* and *Sarcophilus*, rather than the dasyurids with three premolars, such as *Antechinus* and *Sminthopsis*.

Keywords

Thylacinus, marsupials, Dasyuridae, deciduous dentition, dental development, pouch young, homologies

Institutional abbreviations

AM, Australian Museum, Sydney, Australia; AMNH, American Museum of Natural History, New York, New York, USA; CU, Cambridge University, Museum of Zoology, Cambridge, England; LAC, Laboratoire d'Anatomie Comparée, Paris, France; MN, Museum für Naturkunde, Berlin, Germany; NMV, Museums Victoria, Melbourne, Australia; SAM, South Australian Museum, Adelaide, Australia; TMAG, Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia; USNM, United States National Museum, Washington DC, USA, WAM, Western Australian Museum, Perth, Australia

Introduction

Although the last known living specimen of the marsupial *Thylacinus cynocephalus* died in the Hobart Zoo in Tasmania, Australia, on 7 September, 1936, frequent reports of sightings have continued to occur in Tasmania; (see Paddle, 2012, for a recent summary). However, no new living or dead specimens of the thylacine have been found since 1936, and most authorities accept that the thylacine is now extinct. An excellent overview on the biology of *Thylacinus* was provided by Joan Dixon (1989).

The earliest study on the developing dentition of *Thylacinus* known to us was conducted by William Flower (1867), who illustrated a juvenile pouch young with unerupted teeth. In lateral view, Flower showed three (of the four) developing incisors, the canine, three deciduous premolars, a developing successional third premolar (P3), and the developing M1 - 2 in both jaws. A reproduction of his figure is shown in fig. 1. The juvenile specimen was from the Museum of the Royal College of Surgeons of England and the Head Length (HL) measured 71.1 mm.

No teeth had yet erupted above the soft tissues of these jaws; however, Flower's dissection revealed the apex of a small tooth in both the maxilla and dentary, barely elevated above the level of the bone. These small teeth were identified as the third deciduous premolars (dP3), overlying the deeper and less developed third successional premolars (P3). In later stages of all marsupials then known, Flower noted that the underlying and larger successional third premolars would later displace and replace these deciduous predecessors in both jaws.

The tiny dP3 in the upper jaw measured only 2.54 mm in length and lacked distinct roots. The tiny dp3 in the dentary was slightly smaller and also lacked distinct roots. Following

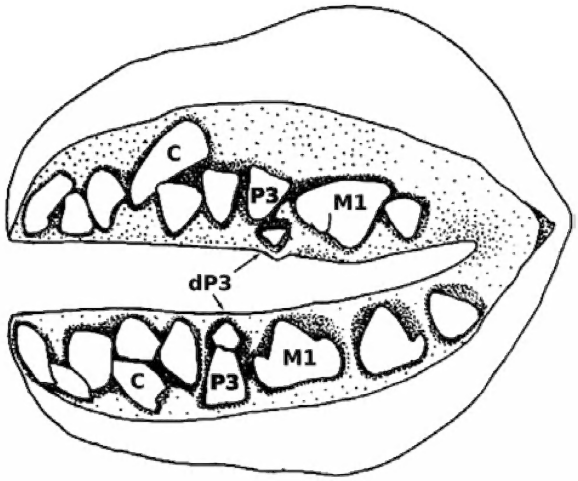

Figure 1. *Thylacinus* (71.1 mm Head Length) pouch young, with unerupted dentition; redrawn from Flower, 1867. C, upper and lower canine; dP3, upper and lower deciduous third premolar; M1, upper and lower first molar; P3, upper and lower successional third premolar.

his examination of *Thylacinus* and representatives of five other families of marsupials, Flower emphasised that the "peculiar condition of dental succession"(Flower, 1867: page 637) in marsupials differed greatly from that in eutherian mammals. This mode of dental development was characterised by tooth succession at only the third premolar position in all marsupials examined by him. Flower therefore considered this condition in marsupials to be a "rudimentary diphyodont condition"(Flower, 1867: page 638), with tooth replacement being confined to a single tooth position on each side of both jaws.

As a closing thought, Flower (1867) suggested that earlier developmental stages of marsupials might show additional evidence for deciduous predecessors at other tooth positions. Later studies by Oldfield Thomas (1887) revealed that variation occurred in dental development within the marsupial family Dasyuridae, with some genera having three premolars (*Thylacinus*, *Sminthopsis* and *Myrmecobius*), whereas others had only two premolars (*Dasyurus* and *Sarcophilus*). Curiously, Thomas called the posterior deciduous premolar and its successor "Pm4," rather than dP3 and P3, considering them to be homologous with the fourth premolars in eutherians. Numerous studies on the developing dentitions of marsupials and eutherians continued during the latter part of the 19th century, although none of these included additional specimens of *Thylacinus*.

Several authors began to use microscopic studies of the marsupial and eutherian dentitions in the 1890s. A significant study by Leche (1893) showed histological sections of early dental development in the dasyurid *Myrmecobius*, in which he described and illustrated the occurrence of small abnormal teeth, which he called "prelacteal" or pre-milk teeth, in the developing incisor and canine regions. Some of these abnormal teeth contained a prominent dentinal nodule and occurred labial to the normal developing first incisor and canine, which were in the late bell stage of development (his figs 1 and 2). This and other related studies on the developing dentition of marsupials were discussed in great detail by Wilson and Hill (1897), in their microscopic study of extensive samples of the developing dentition in the Australian peramelid *Perameles*. One of their major findings was to note that the third deciduous premolar in several genera of marsupials differentiated from the dental lamina contemporaneously with the so-called "prelacteal" or pre-milk teeth in the incisor and canine regions, and they concluded that these teeth belong to the same dental series and were homologous to the deciduous or milk series of eutherians.

In contrast, Wilson and Hill (1897) considered the two premolars anterior to dP3 in both jaws of marsupials to be homologous with the successional third premolars (i.e., to be P1 and P2), although they presented no developmental data to support this hypothesis. These anterior premolars develop later than dP3 in all marsupials studied to date, and they develop directly from the primary dental lamina, as do dP3. We are unaware of any developmental studies that show that these anterior deciduous premolars are replaced by successional teeth. Nevertheless, most studies of fossil and extant marsupials have continued to refer to these teeth as P1 and P2 [see Archer et al.(2016), Murray and Megirian (2006), and Yates (2014, 2015) as recent examples].

In Flower's (1867) study of the juvenile *Thylacinus*, he considered that it belonged in the family Dasyuridae, and he noted that it would be useful to compare its developing dentition with that of Dasyurus and other dasyurids. Numerous studies on dental development in dasyurids have been carried out since then (Archer, 1976; Luckett and Woolley, 1996), although *Thylacinus* was later placed in a separate family Thylacinidae. Today, both morphological and molecular studies group Thylacinidae, Dasyuridae and Myrmecobiidae within the marsupial order Dasyuromorphia (see Archer et al., 2016, and Westerman et al., 2015). Unfortunately, additional studies on dental development in *Thylacinus* were not carried out before the genus became extinct in 1936.

Material and methods

During a trip by one of us (WPL) to Melbourne, Australia, in 1992, to study dental development in a variety of marsupials, numerous specimens of juvenile dasyurids and other Australian marsupials were examined at Museums Victoria. This included several specimens of juvenile thylacines preserved in the alcohol collections of the Mammal Department. One case included a female thylacine and her four pouch young, which had been collected in Tasmania on 23 June, 1909 by W.M. McGowan. The four pouch young and the head of the mother were stored in alcohol. Fortunately, a testis had been sectioned from one of the pouch young by Dr Patricia Woolley of La Trobe University; this indicated that tissue preservation was relatively good. Following discussions between WPL and Joan Dixon, Curator of Mammals at

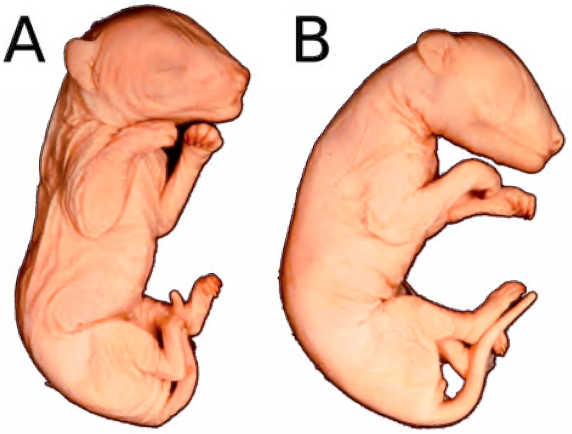

Figure 2. Sibling pouch young thylacines. A, NMV C5754, male specimen sectioned for histology images; B, NMV C 5757, female specimen, used by Feigin et al. (2018) for genomic analysis.

Figure 3. Histological section of I1 in *Thylacinus*, in middle bell stage. dp, dental papilla; en, epithelial nodule; o, oral epithelium; pdl, primary dental lamina.

Museums Victoria at the time, it was agreed that one of these valuable pouch young would be made available for histological investigation. The pouch young (PY) selected for study (NMV C 5754) was a male with a crown - rump length (CRL) of 77.8 mm and a head length (HL) of 34 mm (fig. 2a). The age of this pouch young litter was recently estimated to be 4.5 weeks old (Newton et al., 2018).

We decided to have this valuable pouch young sectioned histologically by our colleague Professor Dr. Milan Klima at the Dr Senckenbergische Anatomie, J.W. Goethe-Universität in Frankfurt am Main, Germany, because of his extensive experience in the preparation and study of histological serial sections from mammalian foetuses and pouch young, including marsupials and whales. Dr. Gerhard Storch at the Senckenberg Natural History Museum in Frankfurt am Main agreed to assume responsibility for this valuable specimen during its preparation in Germany. Following photographs and X-rays, the head of the pouch young was removed and decalcified in 5% HNO_3. It was then embedded in celloidin-paraffin and sectioned serially at 10 um in a transverse (coronal) plane. The resulting 323 slides were stained alternately with azan trichrome, or with haematoxylin and eosin. As a consequence of the unknown fixation of the specimen in 1909, the resulting tissue preparation is only fair. Nevertheless, the histological detail is adequate for the recognition of most soft tissues, the developing dentition and the enamel matrix. There is some loss of bone and of dentin in the sections. In addition to our study of the developing dentition, we anticipated that other aspects of the developing cranium and postcranium might be studied by other collaborators, including Professor Klima. Following our examination of the slides for dental development, the slide series was returned to Museums Victoria.

After preparation of the histological series for dental development, we were assisted by our colleague Dr. Friedemann Schrenk, at the Landesmuseum, Darmstadt, Germany, in photographing the slides.There is some distortion in the specimens, but most details can be recognised. One of us (NHL) made some camera lucida reconstructions from the serial sections to better show the relationships between dP3 and P3 in both jaws. There was no eruption of any teeth in the developing pouch young. For comparison, we show X-ray analysis of an older pouch young (AM P 762) of the thylacine from the Australian Museum in Sydney, which shows very early signs of tooth eruption. Developmental stages and dental homologies follow those described in Luckett (1993a, b) and Luckett and Woolley (1996).

Results

Upper jaw

The first incisor (I1) is a moderately large tooth in the middle bell stage of development, with moderate development of the stellate reticulum (fig. 3). The outer and inner layers of the middle bell are artifactually separated; this may be due, in part, to the lack of dentin and enamel. Development of this tooth is considerably retarded or delayed compared with that of the other developing incisors. The primary dental lamina stalk is relatively intact and attached to the oral epithelium. The premaxillary alveolus for this tooth is relatively shallow, compared with that for I2. Bilaterally, there are tiny buccal epithelial nodules that may represent epithelial remnants of a rudimentary deciduous I1, as are known to occur in many other marsupials (see Leche, 1893). However, this is impossible to corroborate without access to younger developmental stages. Such rudimentary deciduous incisors, often containing dentin, are readily seen in the dasyurids *Sminthopsis virginiae* (Luckett and Woolley, 1996) and *Dasyurus viverrinus* (Luckett et al., unpublished research). For instance, in a *Dasyurus viverrinus* pouch young of 23 mm greatest length, there is a rudimentary dI1 with a distinct tiny epithelial knot associated with a moderately large successor I1 in the middle bell stage.

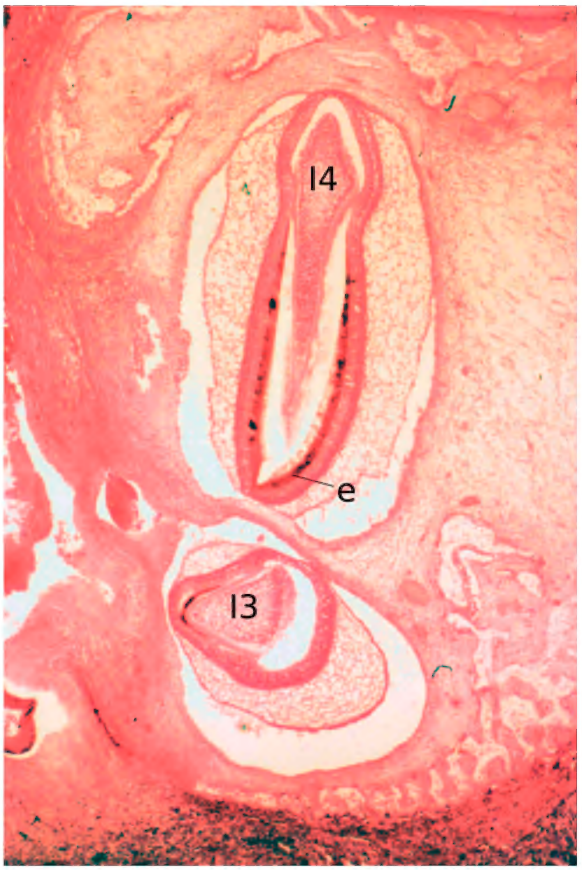

Figure 4. Longitudinal section through I4 and transverse section through smaller I3. e, disrupted enamel.

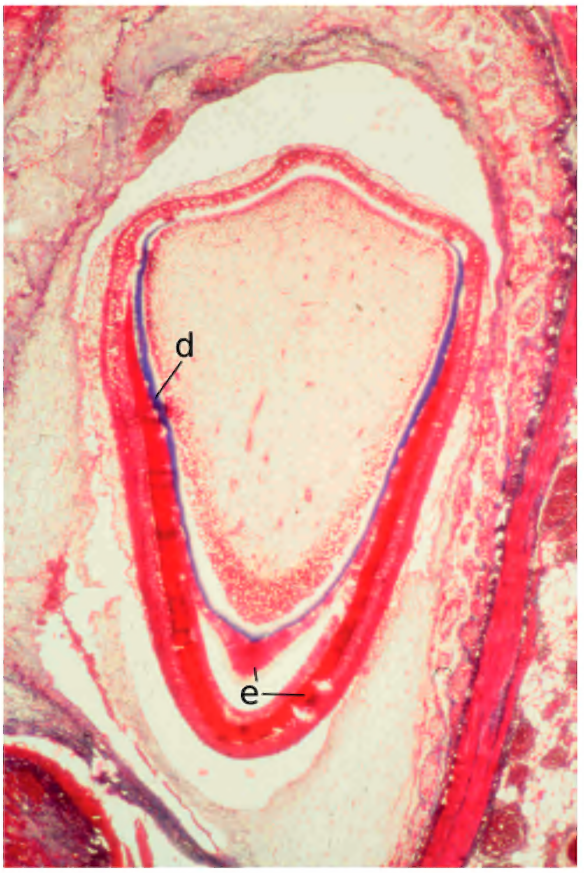

Figure 5. Longitudinal section through large successional upper canine, with disrupted dentin and well -developed enamel. d, dentin; e, enamel.

I2. A large tooth with moderately thick enamel. The dentin was probably moderately thick to thick; however, partial dissolution of dentin in this and other teeth makes this difficult to determine accurately. There are only scattered epithelial remnants of the primary dental lamina, with little if any connections to the oral epithelium. The alveolus for the developing tooth is much deeper than that for I1. There is no evidence of the remains of a rudimentary dI2.

I3. A large tooth, similar in development to I2, with moderately thick enamel and disrupted dentin. The tooth is somewhat procumbent and its enamel is thicker buccally than lingually (fig. 4). There are prominent buccal epithelial nodules on both sides of the jaw; these occur mesio-buccal to I3 and they could be remnants of a rudimentary dI3.

I4. A moderately-sized tooth, smaller than I2 and I3, with moderately developed to moderately thick enamel on its apex (fig. 4). There is no trace of a rudimentary dI4.

Canine. A large vertically implanted tooth, with moderately thick enamel and disrupted dentin (fig. 5). The tooth lies in a deep alveolus at the rostral extent of the maxilla. There are no traces of a rudimentary dC.

dP1. A moderately sized tooth, with relatively thick enamel and disrupted dentin. Its primary dental lamina stalk is detached from the oral epithelium. A short, flattened lingual successional lamina occurs at the mid-level of the tooth.

dP2. A moderately large tooth, with relatively thick enamel and disrupted dentin on the apex of the single cusp (fig. 6). The primary dental lamina stalk is also detached from the oral epithelium. A short flattened lingual successional lamina occurs along the mid-level of the tooth. The tooth lies anterior to the large orbit. A thin distinct layer of connective tissue separates the detached primary dental lamina stalk from the oral epithelium for both dP1 and dP2.

dP3. A small tooth, lying in a shallow alveolus beneath the anterior margins of the orbit. A layer of moderately thick to

Figure 6. Longitudinal section through dP2, with disrupted dentin and well - developed enamel. d, dentin; e, enamel.

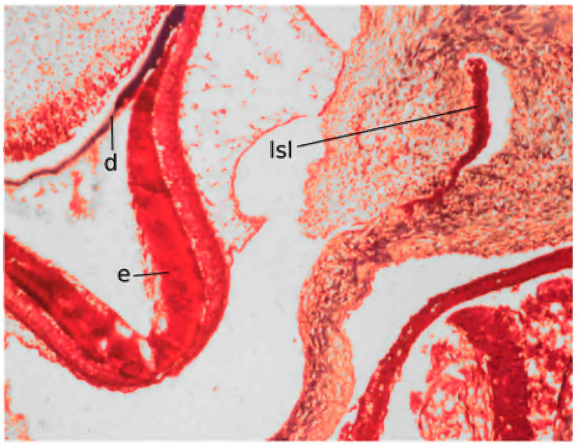

Figure 7. Longitudinal section through the apex of the small dP3, with its disrupted dentin and thick enamel. A segment of its lingual successional lamina is evident, but its attachment to the outer enamel epithelium is not evident in this section. d, dentin; e, enamel; lsl, lingual successional lamina.

Figure 8. Late bell stage successor P3. This tooth lies anterior to dP3 and it lacks dentin and enamel. lsl, short segment of lingual successional lamina; t, tongue.

thick enamel and disrupted dentin overlies the small ovoid cusp (fig. 7). There are only slender fragmented remnants of the detached primary dental lamina stalk. A slender epithelial strand connects the outer enamel epithelium (OEE) of dP3 to its lingual successional lamina at a level near to the middle of the paracone elevation. At this level, the successional lamina appears relatively short in the sections; however, it is continuous with the lamina extending anteriorly to the developing successor P3 (see camera lucida reconstructions of the same relationships between dp3 and p3 in the lower jaw; fig. 11a, b).

Successor P3. A large late bell stage tooth with moderately well-developed stellate reticulum lies immediately anterior to the smaller dP3. There is no distinct evidence for dentin or odontoblasts on the apex of the cusp (fig. 8). The larger P3, although less differentiated than its deciduous predecessor, extends deeper into its developing alveolus than the more superficial disto-buccal and smaller dP3. Only a short segment of the lingual successional lamina is evident in fig. 8. This successional lamina runs parallel to the oral epithelium but is not attached to it. Instead, it extends posteriorly through the sections to its origin on the lingual successional lamina of dP3, in the same manner as it occurs in the lower jaw (see camera lucida fig. 11b).

M1. A large tooth overlapping the distal end of dP3 extends deeper into the jaw than dP3. Only isolated remnants of the primary dental lamina stalk are evident mesially. A moderately elevated mesio-buccal paracone is in the late bell stage but lacks dentin and odontoblasts (fig. 9b). A small spherical epithelial nodule of stratum intermedium cells is detached over the distal extent of the paracone elevation (fig. 9a), similar to the condition that occurs in some dasyurids and *Didelphis*. Detachment of this small epithelial nodule over the paracone, but not over the metacone or protocone, has been suggested to be correlated with the earlier development and

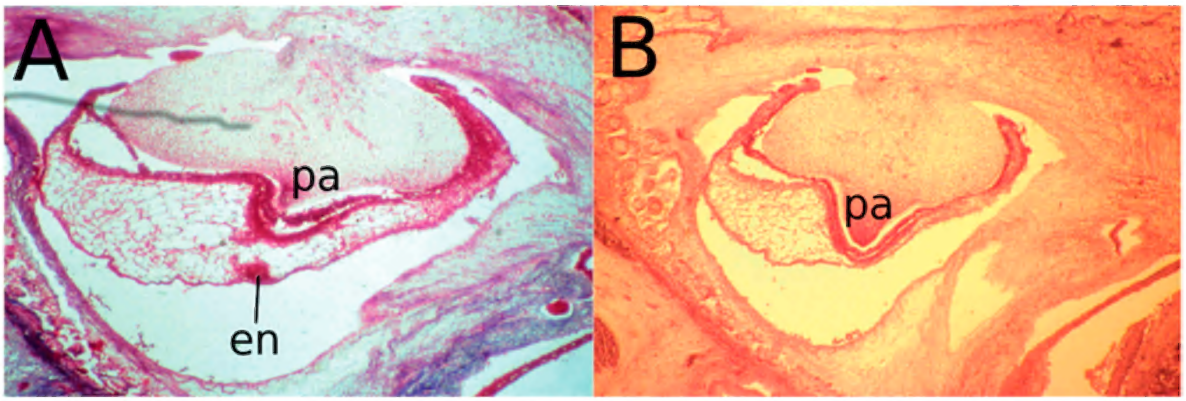

Figure 9. Section of M1, at level of paracone. A, paracone with overlying epithelial nodule; B, paracone at more central level, lacking the epithelial nodule; en, epithelial nodule; pa, paracone apex.

calcification of the taller metacone, in relation to the shorter and later developing paracone in didelphids and some dasyurids (Luckett et al., unpublished research). Presumably, a similar developing condition is also occurring in *Thylacinus*.

A short flat stylar shelf occurs buccally at the paracone level; a broader flat lingual shelf is also present at this level for the future development of a protocone, which is still lacking at this stage. A moderately tall disto-buccal metacone shows greater development, with moderately thick dentin and enamel (fig. 10). In contrast with the paracone, there is no evidence of a detached epithelial nodule over the taller metacone.

M2. Moderately large early-middle bell stage with a moderately developed central epithelial knot developing distal to M1. This tooth occurs beneath the distal 1/3 of the eye. The dental lamina ends distal to this tooth with no trace of a primordium for M3 or M4.

Lower jaw

i1. A large tooth, somewhat procumbent, with moderately thick enamel and dentin. Only isolated remnants of the dental lamina stalk are evident. There is no trace of rudimentary elements for a deciduous precursor for this or other lower incisors.

i2. A large tooth with moderately thick enamel and disrupted dentin.

i3. A moderately large tooth with relatively thick enamel and disrupted dentin.

canine. A very large tooth with moderately thick dentin and enamel, similar to the condition in the upper canine.

dp1.A moderate sized tooth with relatively thick enamel and disrupted dentin on its apex. There is a short flattened lingual successional lamina on both dp1 and dp2, as occurred in the upper jaws.

dp2.A larger tooth with moderately thick enamel; this may be slightly thinner than that on dp1, but this is difficult to determine.

dp3. A small and somewhat elongate tooth, with relatively thick enamel and disrupted dentin on the apex of the tooth (fig. 11a, b). The mesial end of the tooth overlaps the more lingually situated, and larger, successor p3. A nearly intact slender strand of the primary dental lamina stalk extends from the apex of the tooth near its mesial end towards the oral epithelium. Then, larger epithelial islands of the fragmented primary dental lamina stalk continue towards the oral epithelium. There is no direct connection with the oral epithelium, but the intermittent epithelial island remnants make this earlier connection evident (see camera lucida fig. 11b).

A single moderately elevated cusp (probably the protoconid) is evident on the tooth; this becomes reduced distally. There is a slight suggestion of two additional cusps distal to the protoconid, but these are not very distinct. At the level of the middle of the protoconid, a nearly complete slender epithelial strand extends between the greatly thinned outer enamel epithelium of dp3 and the fragmented proximal portion of the lingual successional lamina (see fig. 11b). At this level there are fewer remnants of the primary dental lamina stalk attached to dp3; these are better developed along the mesial third of the tooth. Epithelial strands of the lingual successional lamina continue mesially towards the large developing successor p3.

successor p3. A large, late bell stage tooth, with thin to moderately developed dentin on its apex (fig. 12). The tooth lies lingual to, and somewhat mesial to, the smaller, more superficial dp3 and it extends deeper into the jaw. Ameloblasts are polarised over the cusp, but there is no distinct evidence of enamel. Epithelium of the lingual successional lamina is attached to the apex of p3 and the epithelium runs parallel to the oral epithelium but is not attached to the latter (fig. 11a). The larger p3 extends somewhat mesial to the smaller dp3. The intermittent, and nearly complete successional lamina attachment between p3 and dp3 is best developed on the right side of the jaw (see fig. 11b).

m1. A very large tooth with thick enamel and disrupted dentin on the apex of the tall protoconid. There is no trace of a lingual paraconid mesially. While there are other slight swellings of the epithelium, there is no distinct evidence for other developing cusps.

m2. A large tooth with moderately thick enamel and dentin on the tall mesio-buccal protoconid. There is no evidence for a

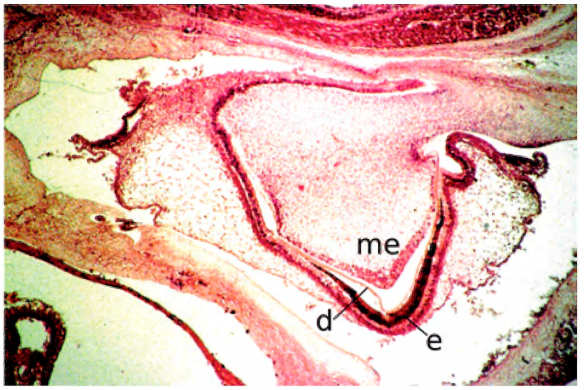

Figure 10. Section through the level of the metacone on M1, with thick enamel on its apex and disrupted dentin; d, dentin; e, enamel; me, metacone apex.

paraconid elevation mesially, or for other developing cusps. There is a short residual lingual lamina at the level of the protoconid.

m3. A moderately large tooth in the middle- late bell stage. The dental lamina disappears distal to this tooth with no evidence of a developing m4.

Other developing stages of the dentition in *Thylacinus*

There has been little, if any, attempt to describe early or later developmental stages of the dentition in *Thylacinus*. One of the few examples was the study by Heinz Moeller (1968), in which he described and illustrated the erupting dentition in a juvenile skull of *Thylacinus*. We have included this specimen in a larger sample of developing dentitions in juvenile and subadult thylacines, collected by one of us (WPL) from several museums in Australia, North America, France and Germany.

The recent discovery of four juvenile thylacine pouch young in the collections of the Charles University in Prague, Czech Republic (Sleightholme et al., 2012), that are even younger than our specimen, raises hopes for the possible further assessment of early development of the rudimentary deciduous incisors and canines in *Thylacinus*, as well as other aspects of their developmental biology. The specimens shown in their photos suggest the possibility that these pouch young are in a poorer state of preservation than our pouch young, and it is unclear as to whether the authors plan to attempt a histological study of one of their pouch young. We hope that they will attempt such a project.

During the preparation of our manuscript, a paper published by Newton et al. (2018) presented X-ray computed tomography scans of five thylacine pouch young specimens, representing all of the known PY litters of *Thylacinus* (see their fig. 2). The emphasis in their study was on growth changes in the cranial and postcranial skeleton; only minimal data were provided concerning the developing dentition in these PY. Their youngest specimen, from the Prague collection (DZCU 8021), was estimated to be 1.5 weeks old (10–11 days). For this pouch young , the authors noted that "two to three tooth sockets are visible in each of the jaw quadrants"(Newton et al., 2018: page 9). They made no attempt to identify or locate the specific developing teeth.

As we will discuss later, *Dasyurus viverrinus* appears to be very close in its pattern of dental development to the conditions in the thylacine, and we have examined two 10–day old PY of *D. viverrinus*, in order to obtain an estimate of the likely dental developmental conditions in the Prague pouch young of 10 –11 days old (Luckett et al., unpublished research). There is evidence of two to three developing teeth in the dasyurid PY, similar to the condition noted for the Prague PY. In the upper jaw of the *Dasyurus* PY, there is a well-developed dP3 in the early–middle cap stage, and a tiny spherical epithelial knot for dC, that is associated with a distinct lingual successional bud for C. There is also a less distinct nodular cap anteriorly for dI2 or dI3, with a disto-lingual successional early bud for I2 or I3. Hopefully, these data would be useful when and if it is possible to examine one of the Prague PY histologically.

The next older pouch young examined by Newton et al. (2018) was estimated to be 35–37 days old (see their Fig. 5) and has an 89 mm CRL (TMAG A931). This PY was considered by the authors to be similar in its development to the Museums Victoria specimens. This would include our 34 mm HL PY and its sister (NMV C5755), examined by them (see their Fig. 2b). Newton et al. chose to examine and describe the TMAG specimen rather than the Museums Victoria PY, because of its apparent better state of preservation. The authors noted the occurrence of several deciduous teeth in both jaws, without further comment or illustrations. However, we were able to examine some aspects of this and the older dentitions of the thylacine PY studied by Newton et al. (2018) due to their inclusion of extensive electronic supplementary material that they made available publicly for study of the dentition and the cranio-skeletal morphology.

Our brief examination of Newton et al.'s (2018) supplementary material for TMAG A931, which is slightly older than our sectioned thylacine PY, revealed the presence of tiny, unerupted dP3 in both jaws, and the apparent very early eruption of the protoconid of m1 above the alveolar margins in the lower jaw (fig. 13a). There was no distinct evidence for any tooth eruption in the upper jaw. The unerupted canine and dP1-3 were evident in both jaws. However, we were unable to see any distinct evidence for the successor P3 in either jaw. We suspect that this is correlated with the development of little or no dentin on the P3 as yet, similar to the condition in our sectioned PY.

The next older pouch young examined by Newton et al. (2018) was a male (TMAG A930), estimated to be about 9.5 weeks old (66 - 67 days), and illustrated in their fig. 6. The authors noted that this specimen contained several unerupted teeth in both jaws but gave no further description of the dentition. Our examination of their supplementary material revealed the presence of tiny dP3 in both jaws; these appear to be erupted above the alveolar margins of both jaws (fig. 13b). These images also show the presence of the unerupted successor P3 in both jaws, in close proximity and immediately anterior to the smaller erupting dP3. The lower dp3 is somewhat more erupted than the upper one, and its successor p3 is also anterior to, but not as closely apposed, to dp3 as is the upper P3.

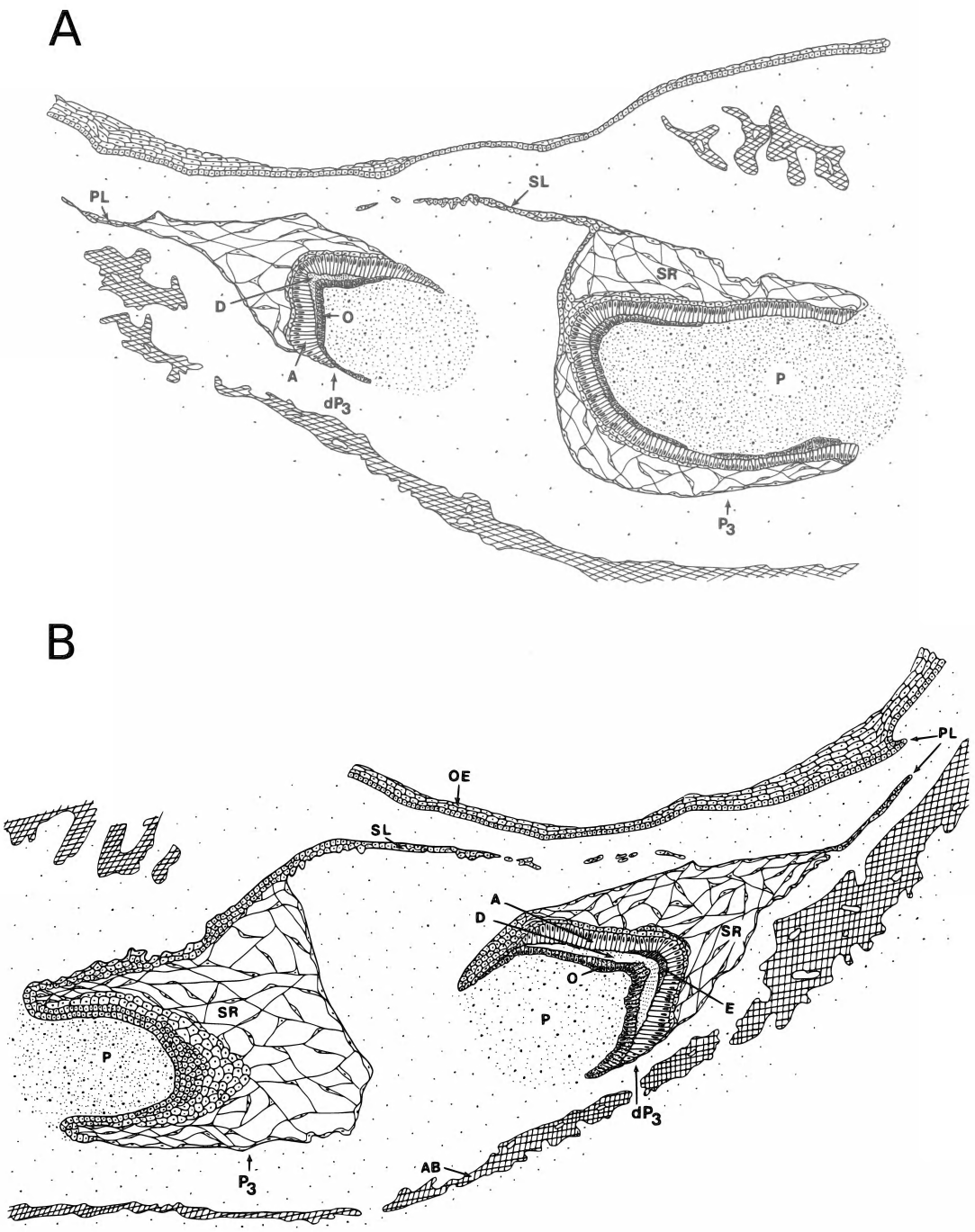

Figure 11. Camera lucida drawings of dp3 and p3 in the dentary, at different planes of section. A, The lingual successional lamina is fragmented, but still largely intact, between the small dp3 and its larger successional p3; B, The small dp3 is evident with its dentin and enamel, and its primary dental lamina connection to the oral epithelium is fragmented but still evident. The section through the successor p3 is not central, but it shows the fragmented lingual successional lamina between the two teeth. A, ameloblasts; AB, alveolar bone; D, dentin; dp3, deciduous third premolar; E, enamel; O, odontoblasts; OE, oral epithelium; P, dental papilla; p3, successor third premolar; PL, primary dental lamina; SL, lingual successional lamina; SR, stellate reticulum.

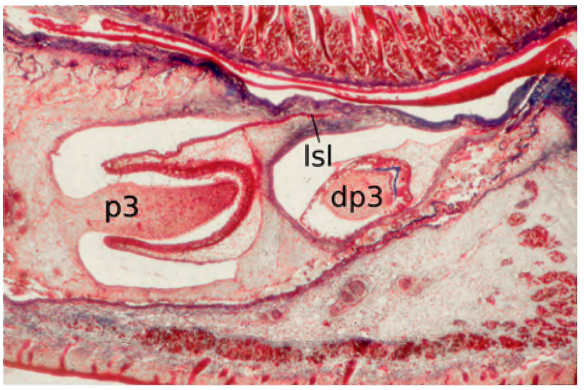

Figure 12. Section through dp3 and its successor p3. Only a small fragment of the lingual successional lamina is evident. Compare this single section with the camera lucida drawings in Figure 11. dp3, deciduous third premolar; lsl, lingual successional lamina; p3, successional third premolar.

Clearly, the complete dentitions of these thylacine PYs should be carefully described and illustrated, and we hope that Newton et al. (2018) will do so in a future publication.

A later stage of tooth eruption in *Thylacinus* available to us is from a pouch young in the Australian Museum in Sydney. This specimen (AM P 762) measured 80.5 mm HL and was collected in Tasmania during 1866 (fig. 14). This PY was recently estimated to be 12 weeks old (Newton et al., 2018). It was not possible to section this young, but we were able to examine the head using X-rays with the help of Dr Lucjan Sych, from the School of Dentistry at the University of Melbourne. The images of the head made by Dr Sych showed that the small spherical dp3 was erupted bilaterally above the alveolar margins in the dentary, with only minimal suggestions of distinct roots (fig. 14a, c). The unerupted, but larger, successor p3 lies immediately anterior to the smaller dp3, as it was in our younger sectioned pouch young and in the TMAG young described above. The apex of dp1 was just slightly above the alveolar margins, whereas the larger dp2 was at or just below the alveolar margins (see fig. 14c). The lower m1 protoconid is in an early stage of eruption above the alveolar margins; m2 is evident within its alveolus but is not yet erupting, as is the less developed m3.

The upper jaw was more difficult to interpret in our X-rays, and it was especially difficult to identify the dP3 and its state of eruption. Fortunately, the recent publication by Newton et al. (2018) on the available thylacine pouch young specimens included X-ray computed tomography scans of AM P 762, and we were able to examine this specimen in greater detail, thanks to their inclusion of extensive supplementary material. We noted that both of the tiny dP3 in the upper and lower jaws were at least partly erupted, with greater eruption in the lower jaw (fig. 15). The unerupted but well-developed successor P3 are also clearly seen immediately anterior and deeper in both jaws, as they were in our younger developing pouch young.

A later stage of dental eruption in *Thylacinus* was described and illustrated by Moeller (1968). We were not able to examine this specimen (CU A6 7/10) from the Cambridge University, Museum of Zoology, but instead relied on the careful description and figures supplied by Moeller (1968). He showed that, in this specimen, I2 - 3 were erupting in the upper jaw, whereas I1 and I4 were unerupted, but evident in their alveoli. This is consistent with our observation of a delayed development of I1 in our sectioned pouch young. Moeller also showed that dP1 and dP2 were in early eruption, but there was no sign of dP3, except for an alveolus that contained the unerupted P3. It is unclear whether the poorly rooted dP3 (probably erupted) was lost or damaged during preparation of the skull. The M1 was unerupted.

In the lower jaw, the canine is unerupted, and dp1 and dp2 are partly erupted, with dp1 being more erupted. A small spherical dp3 is erupted anterior to an erupting m1 (see our reproduction of Moeller's fig. 32a in fig. 16a). The apex of the unerupted p3 is evident in an alveolus anterior to the small dp3. Clearly, Moeller's specimen is only slightly more advanced than our pouch young (AM P 762) from the Australian Museum. A slightly later stage of *Thylacinus* (USNM 115365; skull length = 87.75 mm) shows that dp3 has been lost in the dentary and its successor p3 is in early eruption (fig. 16b). The m1 is almost completely erupted, and m2 is in early eruption. The dp1 is almost completely erupted, whereas the larger dp2 is in an earlier phase of eruption.

Our stages for these and later development and eruption in the upper and lower jaws of *Thylacinus* are presented in Tables 1 and 2. Included in specimens from the dentary we have presented some samples of fossil *Thylacinus cynocephalus* from caves in Western Australia. Radiocarbon analysis of charcoal samples from the Henschke Fossil Cave suggests that the cave was filled in between 32,000 and 40,000 years ago, trapping the thylacines and many other marsupial species within (Pledge, 1990). Although these dentitions are in most cases somewhat smaller than the more recent Tasmanian thylacines, the developmental stages appear to be identical in both groups. For instance, both p3 and m3 are erupting at about the same time in the lower jaw.

Comparison of the thylacine pouch young with similar developmental stages in dasyurids

In comparing our single specimen of the thylacine pouch young with comparable developmental stages of dasyurids, presumably one of its closest relatives within the order Dasyuromorphia, it was interesting to note the occurrence of both similarities and differences within the family Dasyuridae. Unfortunately, we were unable to find a similar developmental stage of *Myrmecobius* (the single representative of Myrmecobiidae) in our studies.

In Table 3, the thylacine pouch young has the successor P3 in the late bell stage, and M2 is in the early - middle bell stage in the upper jaw. The closest similar developmental stage in our dasyurid sample is *Dasyurus viverrinus*, a species in which dP2 has been lost in both jaws (as in all species of *Dasyurus* examined by us). The *Dasyurus* PY has a 13.5 mm HL and its P3 is in the late bell stage, with a thin layer of dentin. Its M2 is in the middle - late bell stage. Given the slightly older specimen of *Dasyurus*, it is quite similar in its developmental stage to our

Table 1. Development and eruption of the upper postcanine dentition in *Thylacinus cynocephalus*, (HL = Head Length).

Stage	dP^1	dP^2	dP^3	P^3	M^1	M^2	M^3	M^4
NMV C 5754 34 mm HL pouch young; no teeth erupting; estimated 31 - 32 days	Moderately thick enamel on apex; flat, short lingual successional lamina	Moderately developed to moderately thick enamel on apex; short lingual successional lamina	Tiny tooth, with moderately thick enamel; fragmented lingual successional lamina extends anteriorly	Large, late bell stage, no odontoblasts; lingual and mesial to tiny dP3	Large tooth, with moderately thick enamel on tall metacone	Moderately large tooth, in early -middle bell stage	No trace	No trace
71.1 mm HL pouch young (Flower, 1867) Museum of the Royal College of Surgeons	Tooth calcified; not erupting	Tooth calcified; not erupting	Tiny, rootless tooth; apex just above alveolar margins (2.54 mm in length)	Tooth deep in jaw; beneath and slightly lingual to tiny dP3	Well calcified tooth; not erupting	Partly calcified tooth; not erupting	Not evident	Not evident
60 mm HL TMAG 930 Estimated 66 –67 days	Calcified tooth; not erupting	Calcified tooth; not erupting	Tiny tooth erupted	Tooth evident but not erupting; anterior to dP3	Tooth not erupting; close to alveolar margins	Tooth not erupting	Not evident	Not evident
80.5 mm HL AM P 762 Haired pouch young; estimated 84 days	Apex of tooth erupting slightly above alveolar margins	Apex of larger tooth just below alveolar margins; not erupting	Tiny tooth erupted	Apex of unerupted tooth evident mesio-lingual to tiny dP3	Tooth evident but not erupting	Tooth evident but not erupting	Not evident	Not evident
Skull length = 80 mm Cambridge Univ. A6 7/10	Tooth erupting	Tooth erupting	Tiny tooth not evident; probably lost	Tooth evident in alveolus, but not erupting	Tooth not erupting	Not evident	Not evident	Not evident
USNM 115365 Juvenile female (skull length = 87.75 mm)	Tooth almost completely erupted	Moderately large; about 2/3 erupted (less erupted than dP1)	No trace	Large tooth; very early erupting, just above alveolar margins	Large tooth; early erupting (about 1/4)	Not evident	Not evident	Not evident
MN Berlin An 13914 Juvenile (skull length = 129.4 mm)	Tooth erupted	Tooth erupted	No trace	Large tooth; almost completely erupted	Large tooth; erupted	Large tooth erupting (about 3/4)	Partially calcified tooth; evident deep in alveolus	Not evident
SAM M1958 Juvenile male (skull length = 130 mm)	Erupted	Erupted	No trace	Erupted	Large tooth; erupted	Large tooth almost completely erupted	Not evident	Not evident
NMV C 5744 Juvenile male (skull length = 157 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Evident in alveolus; not erupting	Not evident
AM P 778 Juvenile (skull length = 159.4 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Early emergence above alveolar margins	Not evident

Stage	dP^1	dP^2	dP^3	P^3	M^1	M^2	M^3	M^4
SAM M1956 Juvenile (skull length = 149 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Early emergence above alveolar margins	Not evident
NMV C 5743 Juvenile (skull length = 153.5 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Early erupting (less than 1/3)	Not evident
NMV C 5600 Juvenile female (skull length = 153.8mm); born in zoo; 18 months old	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Early erupting (about 1/4)	Not evident
AM P778 Juvenile (skull length = 159.4 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Early emergence above alveolar margins	Not evident
MN Berlin A 1745 Juvenile (skull length = 168 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupting (about 1/2)	Not evident
AMNH 77701 Juvenile (skull length = 191.2 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Almost completely erupted	Not distinct; alveolus only
WA F6358 Subadult fossil (skull length = 138.2 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Region damaged; uncertain
AM S1180 Subadult; skull length = 180 mm	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Early eruption (about 1/4)
AM 775 Subadult; skull length = 182 mm (collected 1866)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	About 1/3 erupted
LAC A 3298 Adult; skull length = 192 mm	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Erupted
Other adult skulls, with all teeth erupted; with skull lengths from 192 mm to 253mm								

Table 2. Development and eruption of the lower postcanine dentition in *Thylacinus cynocephalus*, (HL = Head Length).

Stage	dp_1	dp_2	dp_3	p_3	m_1	m_2	m_3	m_4
MV C 5754 34 mm HL pouch young; no teeth erupting; sectioned histologically estimated 31 - 32 days old	Moderately thick enamel on apex; short flat lingual successional lamina	Moderately thick enamel on apex; short flat lingual successional lamina	Tiny, elongate tooth, with moderately thick enamel; lingual successional lamina extends mesial to larger P3	Large, late bell, with moderately developed dentin; lingual and mesial to smaller dp3	Large tooth, with thick enamel on tall protoconid	Large tooth, with moderately thick enamel on tall protoconid	Moderately large, middle-late bell stage; dental lamina ends distal to it	No trace
71.1 mm HL pouch young (Flower, 1867)	Calcified tooth; not erupting	Calcified tooth; not erupting	Tiny, rootless tooth; apex just above alveolar margins	Tooth deep in jaw; beneath and slightly lingual to tiny dp3	Well calcified tooth; not erupting	Partly calcified tooth; not erupting	Partly calcified tooth; not erupting	Not evident
TMAG A930 60 mm HL; estimated 66–67 days old	Probably not erupting; region damaged	Apex of large tooth near alveolar margins	Tiny tooth erupted	Unerupted tooth apex evident mesial to tiny dp3	Tooth at alveolar margins, not erupting	Tooth evident but not erupting	Apex evident but not erupting	Not evident
AM P 762 80.5 mm HL Haired pouch young; estimated 84 days old	Apex of tooth erupting just above alveolar margins	Apex of larger tooth just above alveolar margins	Tiny spherical tooth; erupted above the alveolar margins	Apex of unerupted tooth evident mesio-lingual to tiny dp3	Protoconid of large tooth in early eruption	Apex of tooth evident just below alveolar margins, but not erupting	Partly calcified tooth deep in jaws, not erupting	Not evident
Cambridge University A6 7/10 80 mm skull length (Moeller, 1968)	Tooth almost completely erupted	Tooth partially erupted (about 1/3)	Tiny tooth erupted above alveolar margins	Apex of unerupted tooth evident mesio-lingual to tiny dp3	Protoconid of large tooth in early eruption	Protoconid apex just below alveolar margins; not erupting	Tooth not erupting	Not evident
WAM 72.1.1149 Juvenile fossil right dentary, Murray Cave, Western Australia	Alveolus only; at least partially erupted	Early erupting (about 1/3)	No trace	Apex of unerupted tooth just below alveolar margins	Alveolus only (probably erupted)	Early erupting; slightly less than that of dp2	Not evident	Not evident
USNM 115365 Juvenile female; skull length = 87.75 mm	Tooth erupted	Tooth erupting (about 1/2)	No trace; possible shallow buccal alveolus for lost tooth	Early eruption just above alveolar margins	Large tooth; erupted	Large tooth; early eruption (1/3)	Unerupted tooth in alveolar crypt	Not evident
SAM P 33482 Juvenile fossil dentary, Henschke Fossil Cave, South Australia	Partial alveolus only	Double rooted alveolus only for erupting (or erupted) tooth	No trace	Erupting tooth (about 1/2)	Alveolus only for erupted tooth	Alveolus only for erupting (or erupted) tooth	Erupting tooth (about 1/3)	Not erupting
WAM 61-2-26 Juvenile fossil left dentary, Mammoth Cave, Western Australia	Region missing	Tooth erupted	No trace	Tooth erupting (about 3/4)	Alveolus only for erupted tooth	Alveolus only for erupted tooth	Erupting tooth (about 1/2)	Not distinct

Stage	dp_1	dp_2	dp_3	p_3	m_1	m_2	m_3	m_4
Roaches Rest Cave, fossil 67-3-21	Region missing	Tooth erupted	No trace	No trace; probably erupted	Tooth erupted	Tooth erupted	Erupting tooth (about 2/3)	Unerupted, in deep alveolus
Berlin An 13914 Juvenile skull and dentary (skull length = 129.4 mm)	Erupted	Erupted	No trace	Almost completely erupted	Erupted	Erupted	Partially erupted (about 1/2)	Partially calcified; unerupted, deep in alveolus
SAM 1958 Juvenile skull and dentary (skull length = 130 mm)	Erupted	Erupted	No trace	Completely erupted	Erupted	Erupted	Partially erupted (about 1/2)	Not evident
MV C 5744 Juvenile skull and dentary (skull length = 157.1 mm) male	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Completely Erupted	Early emergence of protoconid above alveolar margins
SAM M1956 Juvenile skull and dentary (skull length = 149 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Very early eruption above alveolar margins
LAC, Paris 1883-352 Juvenile skull and dentary damaged (Collected in 1844)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Very early eruption of protoconid
MV C 5743 Juvenile female (skull length =153.5 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Early eruption (about 1/4)
AM P 778 Juvenile (skull length = 159.4mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Early erupting (about 1/4)
MN Berlin A 1745 Subadult (skull length = 168 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Erupting (about 3/4)
WAM F6358 Subadult fossil (skull length = 138.2 mm) Nullabor Plain, Western Australia	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Erupting (about 3/4)
AMNH 77701 Subadult (skull length = 191.2 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Almost completely erupted
AM 775 Subadult (skull length = 182 mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Erupted (upper M4 still erupting)
MV C 5748 Adult female (skull length = 192mm)	Erupted	Erupted	No trace	Erupted	Erupted	Erupted	Erupted	Erupted (all teeth erupted in both jaws)

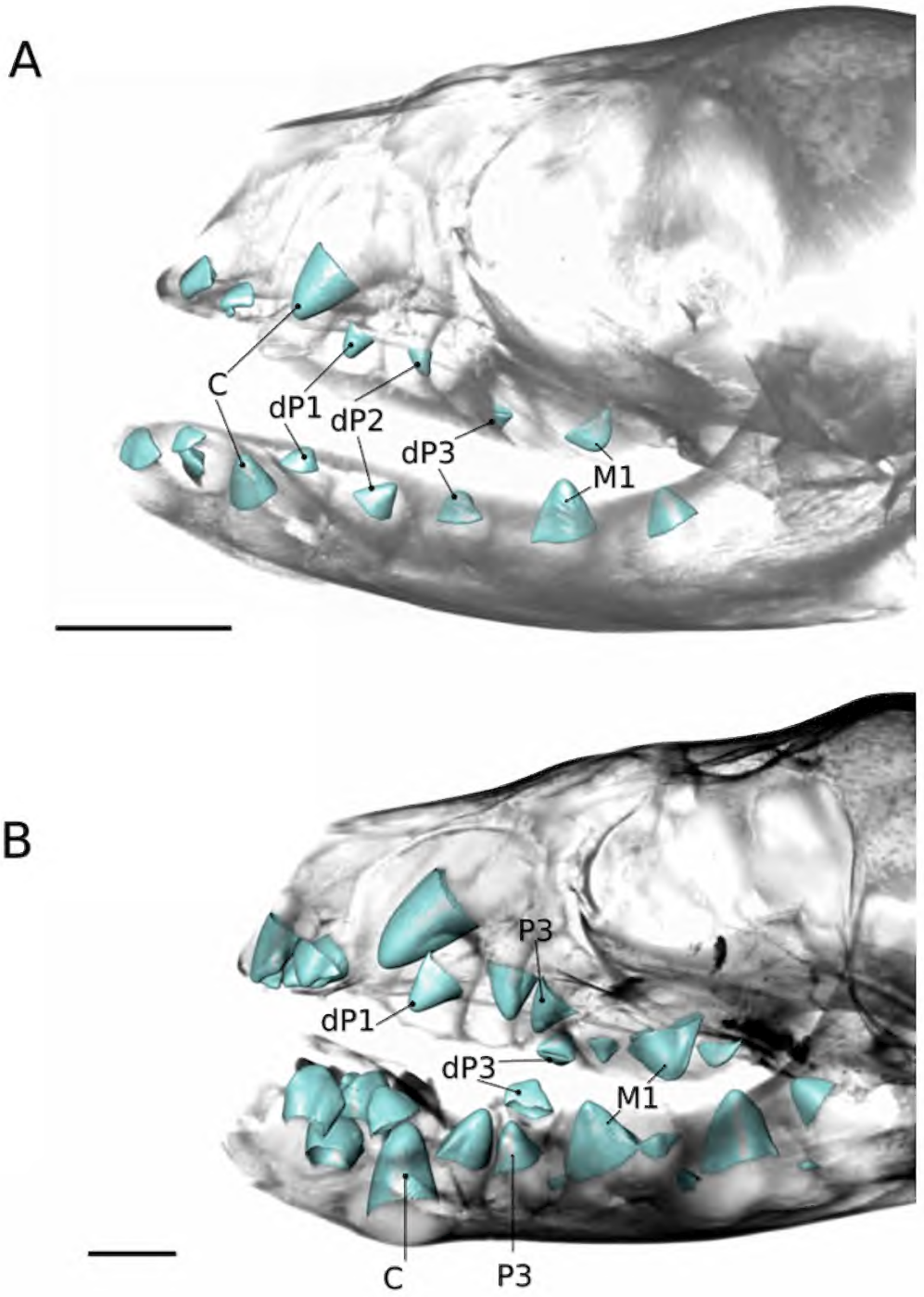

Figure 13. Computed tomography images from the supplementary data of Newton et al. (2018). A, section of the skull and dentition from TMAG A931, a thylacine pouch young of 35 - 37 days old; B, Section of the skull and dentition from TMAG A930, a thylacine pouch young of 66 - 67 days old. Scale bars are 5 mm. C, canine; dP1, deciduous first premolar; dP2, deciduous second premolar; dP3, deciduous third premolar; M1, first molar; P3, successional third premolar.

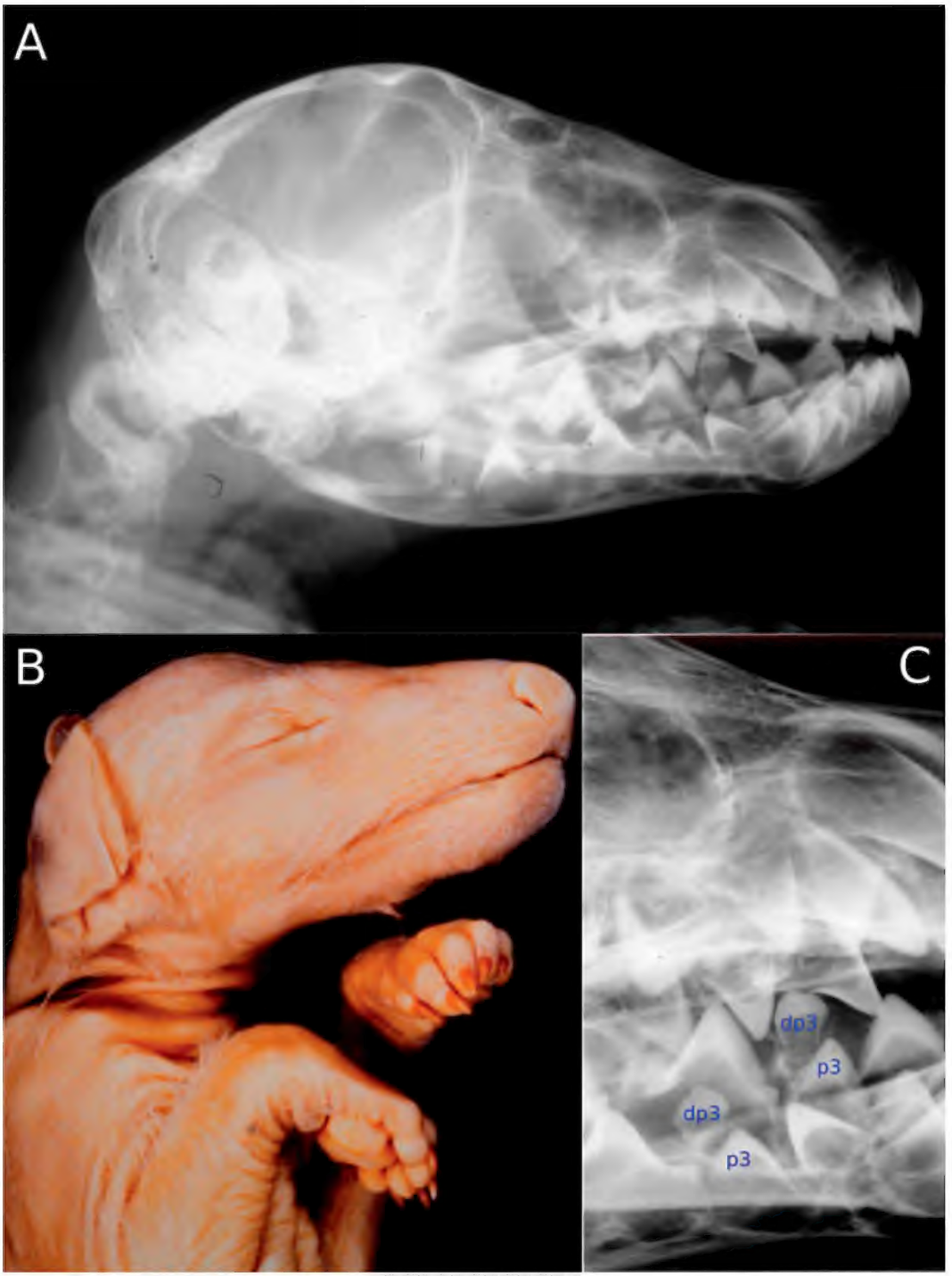

Figure 14. Images of the head, skull, and dentition of the thylacine pouch young from the Australian Museum (AM P 762). A, X-ray of the skull, showing deciduous and successional teeth in varying stages of development and early eruption; B, Head and upper body of the pouch young, prior to X-ray analysis; C, Higher magnification of a portion of the X-ray shown in figure A, with emphasis on the erupted lower dp3, and the unerupted but larger successional p3 immediately anterior to it.

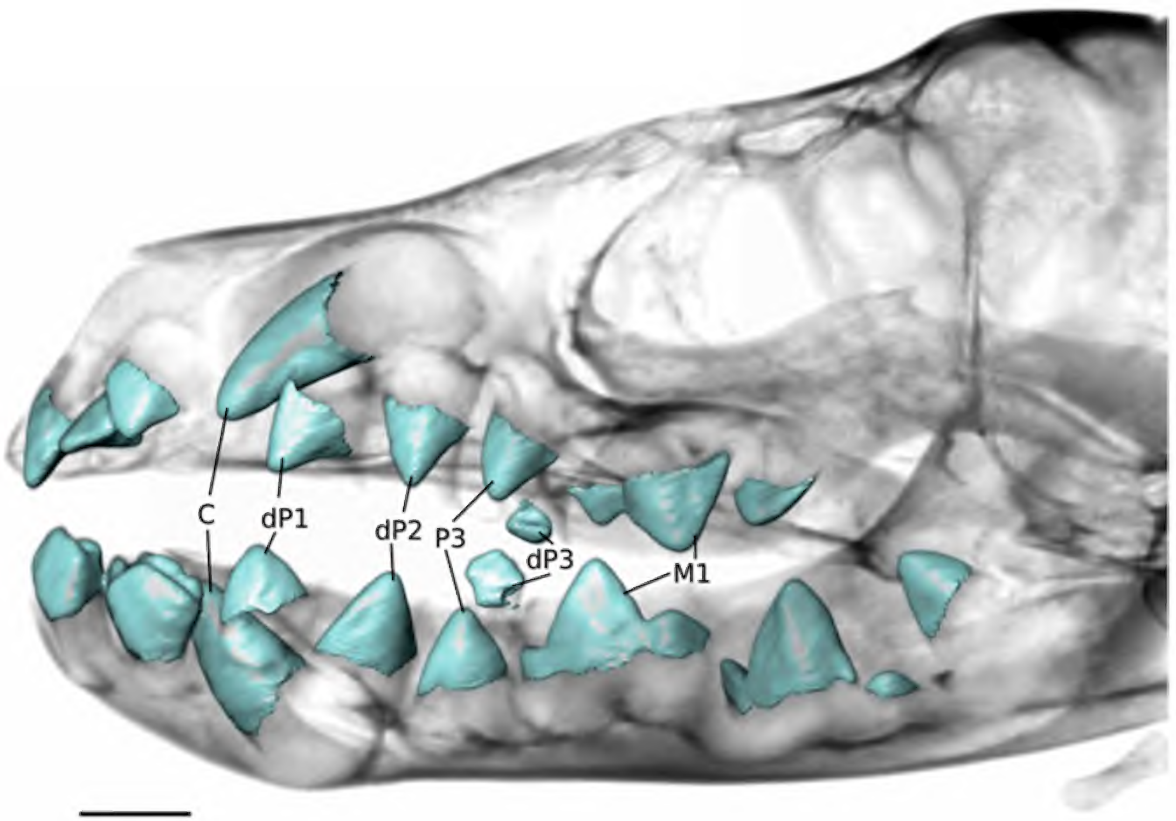

Figure 15. Computed tomography image of the skull and dentition of AM P 762, taken from the supplementary data of Newton et al. (2018). The figure clearly shows the erupted dP3 in both jaws, and the unerupted successor P3 immediately anterior to their predecessors. Scale bar equals 5 mm. Other early erupting and unerupted teeth are clearly labeled. C, successional canine; dP1, deciduous first premolar; dP2, deciduous second premolar; dP3, deciduous third premolar; M1, first molar; P3, successional third premolar.

Thylacinus PY. In the lower jaw, *Dasyurus viverrinus* is also more similar in its developmental stages of the dentition with *Thylacinus* than with the dasyurids with three premolars, *Antechinus* and *Sminthopsis* (see Table 4). Note that there is an accelerated phase of dental development in the lower jaw, compared with that in the upper jaw for both *Thylacinus* and *Dasyurus*. Thus, the lower p3 is most similar with m3 in its developmental stage, rather than with m2.

In contrast, the two dasyurid genera with three premolars that we examined (*Antechinus* and *Sminthopsis*), are quite different and considerably delayed or retarded in the development of their successional P3, compared with *Thylacinus* and *Dasyurus*. Thus, in *Antechinus*, the successor P3 is only suggested by the slight swelling of the lingual successional lamina of dP3, and *Sminthopsis* has P3 in a very early bud stage in the upper jaw (Table 3). However, the M2 of both genera with three premolars are in a similar middle - late bell stage. Note that the differences occur only in the development of the premolars, and not the molars.

Although early developmental stages of *Myrmecobius* were not available to us for comparison with the thylacine 34 mm HL PY, we were able to compare later stages of development of *Myrmecobius* with comparable stages of *Thylacinus* from our Tables 1 and 2. In the upper jaw of a juvenile *Myrmecobius* (WAM M 19214, with skull length = 41.66 mm), P3 was about half erupted and M2 was almost completely erupted. In the lower jaw, p3 was about 3/4 erupted and m3 was erupting. These relationships are most similar to those of a juvenile *Thylacinus* from the Berlin Museum (MN 13914; skull length = 129.4 mm). In the upper jaw of the Berlin thylacine, P3 is almost completely erupted and M2 is about 3/4 erupted (see Table 1). In the lower jaw, p3 is almost completely erupted and m3 is about 2/3 erupted (see Table 2). These relationships suggest that *Myrmecobius* is most similar in its dental development to the dasyurids with two premolars and with *Thylacinus*, rather than with the dasyurids with three premolars, despite the fact that *Myrmecobius* has three premolars in both jaws.

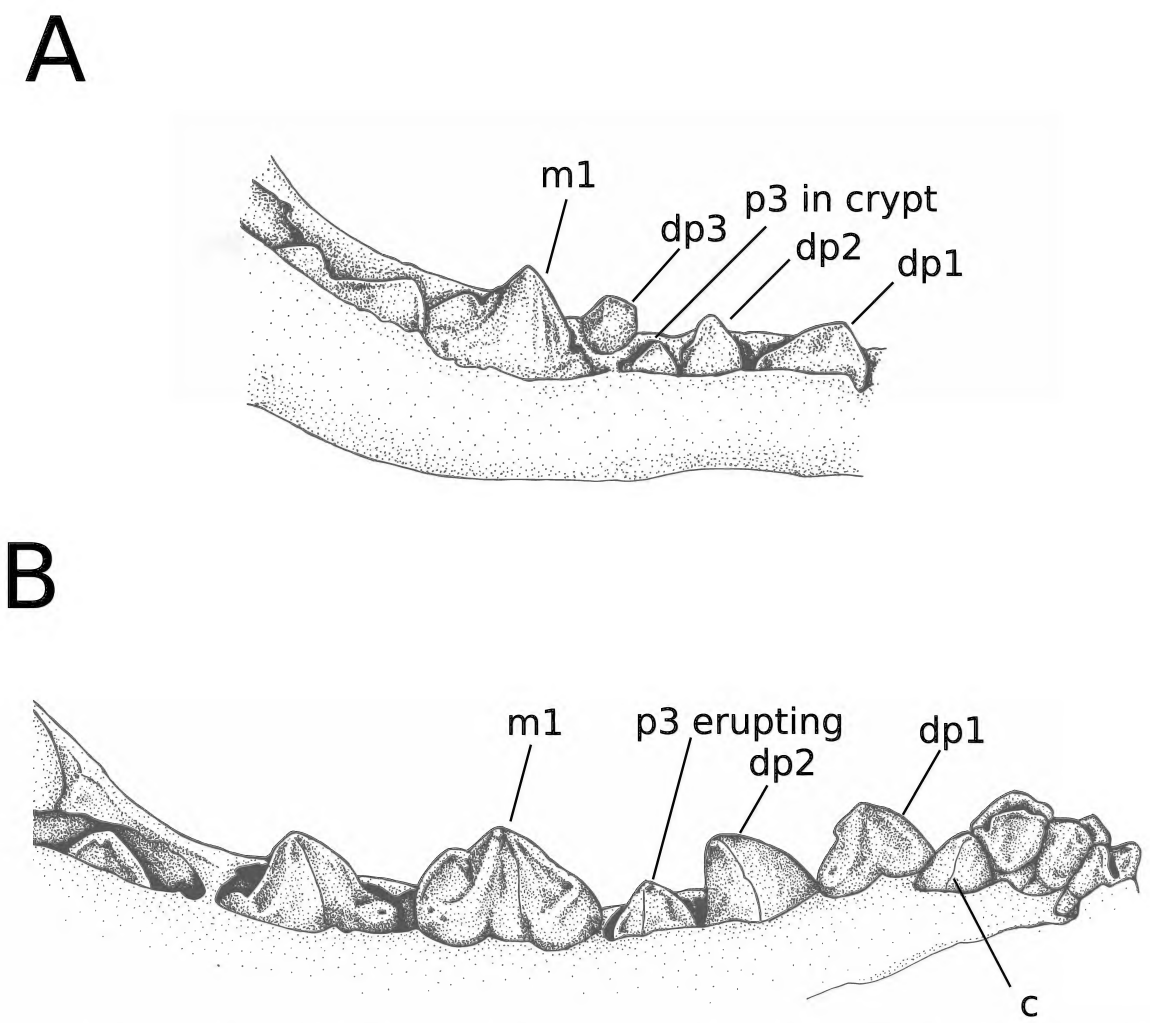

Figure 16. Later stages of early eruption in *Thylacinus* showing the presence and early loss of dp3 in the dentary. A, Part of the dentary (CU A6 7/10), redrawn from Moeller (1968), showing the erupted dp3, the unerupted successor p3 in its alveolar crypt, immediately anterior to dp3, and the erupting m1. The erupting dp1 and dp2 are also labeled; B, A slightly later stage of eruption in the dentary (USNM 115365) shows that the dp3 has been lost, and successor p3 is in early eruption. The m1 is now almost completely erupted. c indicates lower successional canine in B.

We were also able to examine a similar later stage of development in *Sarcophilus harrisii* (AMNH 65674), a dasyurid with two premolars, for comparison with *Thylacinus*. As in other dasyurids with two premolars, and in the thylacine, dental development is accelerated, with dP1, P3, and M1 - 2 erupted in both jaws. In the lower jaw, m3 is almost completely erupted. Although most authors have concluded that it is dP3 (and P3) that is the missing tooth in *Sarcophilus* (Archer, 1976; Tate, 1947; Thomas, 1877; Wroe, 1999), our developmental studies have demonstrated the presence of dP3 and P3 in both jaws of *Sarcophilus*, as well as the absence of a developing dP2 in both early and later stages, similar to the condition in *Dasyurus* (Luckett et al., unpublished research).

For an additional comparison, we examined one specimen of Peramelidae (*Perameles sp.*) and one Didelphidae (*Monodelphis domestica*). Both were similar in developmental stages to the dasyurids with three premolars (see Tables 3, 4). The successor P3 for *Perameles sp.* (16 mm HL) was in the early bud stage, and M2 was in the late bell stage with early odontoblasts in the upper jaw. In the lower jaw, *Perameles sp.* was in the early bud stage for p3, and m3 was in the late bell stage, with early odontoblasts. In *Monodelphis domestica* (14.5 mm HL), P3 was in the early - middle bud stage and M2 was in the late bell stage in the upper jaw. In the lower jaw, p3 was in the late bud - early cap stage and m3 was in the middle bell stage. Note that the molars are in similar developmental stages for all taxa examined, whereas it is the successional P3 that varies in both jaws.

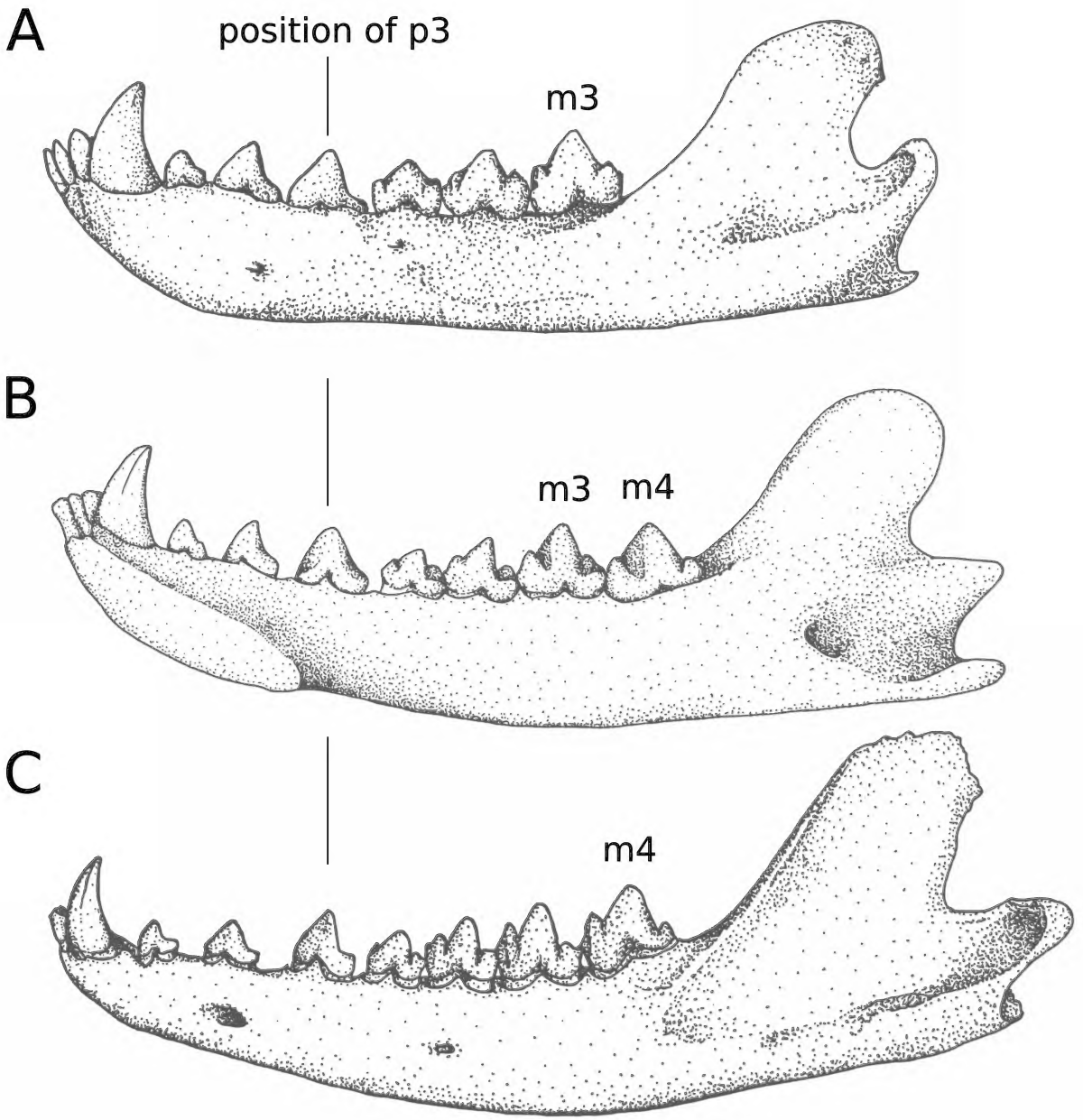

Figure 17. Selected dentaries of *Thylacinus* showing differences in the diastemata between the premolars as the effect of increasing age. A, subadult (in labial view) with m3 erupted, but not m4. Only slight suggestions of diastemata are evident between the premolars; B (lingual view) and C (labial view), showing later stages of m4 eruption and the increase of diastemata in adults.

Relationship of paracone and metacone in thylacines and other marsupials

In *Thylacinus cynocephalus*, the metacone is larger than the paracone on M1 - 3. A similar condition has been found also in numerous Late Oligocene–Miocene fossil thylacinids, including *Nimbacinus* (Muirhead and Archer, 1990), *Badjcinus* (Muirhead and Wroe, 1998), *Wabulacinus* (Muirhead, 1997), *Ngamalacinus* (Muirhead, 1997) and *Mutpuracinus* (Murray and Megirian, 2006). It is likely that a similar condition to that discovered in *Thylacinus* and didelphids, in which the apical

Table 3. Comparison of development in *Thylacinus* and Dasyuridae upper postcanine dentitions, (HL = Head Length).

Taxon	dP^1	dP^2	dP^3	P^3	M^1	M^2	M^3	M^4
Thylacinus (34 mm HL) estimated 31 - 32 days	Moderately thick enamel	Moderately developed to moderately thick enamel	Tiny tooth; moderately thick to thick enamel; shallow bony alveolus	Large, late bell stage; no odontoblasts; deeper bony alveolus	Large tooth; moderately thick dentin and enamel on tall metacone	Moderately large, early - middle bell stage	No trace	No trace
Dasyurus viverrinus (13.5 mm HL) About 35 days	Moderately thick dentin and enamel	No trace	Small tooth; moderately thick dentin; thin enamel; shallow bony alveolus	Late bell stage; thin dentin on apex	Large tooth; moderately thick dentin, thin enamel on tall metacone	Moderately large, middle -late bell stage	No trace	No trace
Antechinus stuartii (9.5 mm HL) 34 days	Moderately thick dentin; moderately developed enamel	Middle - late bell stage	Moderately thick dentin and enamel	Slight swelling of lingual successional lamina	Moderately thick dentin; moderately developed enamel	Middle - late bell stage	No trace	No trace
Sminthopsis virginiae (8.8 mm HL) 30 days	Moderately developed dentin; thin enamel	Late bell stage	Moderately thick dentin and enamel	Early bud stage	Moderately thick dentin; moderately developed enamel	Late bell stage	Early bud stage	No trace
Perameles sp. 16 mm HL	Moderate sized, late bell; possible early odontoblasts	Moderate sized, late bell stage; thin dentin	Moderate sized, late bell; moderately developed dentin	Small early bud stage	Large tooth, with moderately thick dentin and moderately developed enamel	Large, late bell with thin dentin	Small, early - middle bud	No trace
Monodelphis domestica (14.5 mm HL)	Well-developed dentin and enamel	Well-developed dentin and enamel	Large tooth; welldeveloped dentin and enamel	Small early –middle bud	Large tooth; moderately thick dentin and enamel	Moderately large late bell, with moderately developed dentin	Early bud stage	No trace

epithelial nodule is detached from the developing paracone but not from the metacone, is a causative factor in this relationship. It would be interesting to know whether some Oligocene - Miocene thylacinids also had a more molariform and functional dP3, with a tall metacone, than in *Thylacinus cynocephalus*. Unfortunately, we are unaware of any findings of a dP3 in these earlier fossil thylacinids .

Some comments and criticisms concerning similarities and differences between thylacines and other dasyuromorphians and with marsupials in general

It is often noted that *Thylacinus cynocephalus* differs from other thylacinids because of the pronounced diastema between the premolars in its adult dentitions. Indeed, in some cases this has been used in character analyses within thylacinids and other dasyuromorphians (see Muirhead and Wroe, 1998; Yates, 2014). This, however, is simply a factor that increases with age in *Thylacinus cynocephalus*. If we examine some younger juvenile to subadult stages, as shown in Figure 17a, there are few, if any, spaces separating dp1 dp2, and p3. In a juvenile (NMV C 5744; skull length = 157.1 mm) in which dP1 - 2, P3 and M1 - 2 are erupted in both jaws, and m3 is erupted in the lower jaw, the diastema in the upper jaw measured 2.0 mm between dP1 and dP2, and also between dP2 and P3. In the lower jaw, dp1 and dp2 are separated by a diastema of 1.5 mm, as are dp2 and p3. With increasing age and completion of eruption of M4 in both jaws, there is an increase in the length of the diastemata (Fig. 17b, c). We have examined and measured the diastema in a large number of subadult and adult thylacines (measuring192 mm to 253 mm skull length for the adults with all teeth erupted), and this clearly demonstrates that these diastemata increase with age, between the premolars, but not between the molars. As an example, in the oldest (i.e, largest) adult skull examined by us (AM P 767, measuring

Table 4. Development of *Thylacinus cynocephalus* and dasyurid lower postcanine dentitions, (HL = Head Length).

Taxon	dp_1	dp_2	dp_3	p_3	m_1	m_2	m_3	m_4
Thylacinus cynocephalus NMV C 5754 34 mm HL; estimated 31 - 32 days	Moderate sized, thick enamel and disrupted dentin	Moderately large, with thick enamel and disrupted dentin	Tiny tooth, with thick enamel and disrupted dentin; single distinct cusp	Large, late bell stage; thin to moderately developed dentin	Large tooth; thick dentin and enamel on protoconid	Large tooth; moderately thick dentin and enamel on protoconid	Moderately large, middle - late bell stage	Not developed
Dasyurus viverrinus 23 - 25 mm GL (35 days)	Moderately developed dentin, thin enamel	No trace	Tiny abnormal tooth; moderately thick dentin; thin enamel	Early - middle bell; mesial to abnormal dp3	Moderately thick dentin; moderate developed enamel	Moderately thick dentin; thin enamel	Middle - late bell stage	Not developed
Sminthopsis virginiae 10 mm HL (35 days)	Moderately thick dentin, thin enamel	Thin dentin; no enamel	Moderately thick dentin, thin enamel	Slight swelling of lingual successional lamina	Moderately thick dentin; thin enamel	Moderately thick dentin; thin enamel	Middle - late bell stage	Not developed
Antechinus stuartii 9.5 mm HL (34 days)	Moderately thick dentin, moderately developed enamel	Middle-late bell stage	Moderately thick dentin, moderately developed enamel	Slight swelling of lingual successional lamina	Thick dentin, moderately thick enamel	Moderately thick dentin, moderately developed enamel	Middle - late bell stage	Not developed
Perameles nasuta 35 mm GL (16 mm HL)	Moderately large, late bell; very thin dentin	Moderately large, late bell; early odontoblasts	Small tooth; late bell; thin dentin	Lingual early bud	Large tooth; dentin and moderately developed enamel on protoconid	Large tooth; dentin and thin enamel on protoconid	Moderately large, late bell, with early odontoblasts	Not developed
Monodelphis domestica 49 mm CR (16.5 mm HL)	Moderately sized tooth; moderately thick dentin and enamel	Large caniniform tooth; thick dentin and enamel	Large tooth; thick dentin and enamel on tall protoconid	Small late bud - early cap; mesio-lingual to dp3	Large tooth; thick dentin and enamel on tall protoconid	Large tooth; thick dentin and enamel on protoconid	Moderately large tooth, in middle bell stage	Not developed

about 253 mm skull length), the teeth were heavily worn, and the diastema in the upper jaw measured 3.3 mm between dP1 and dP2, and 4.9 mm between dP2 and P3. In the lower jaw, the diastema was 5.2mm between dp1 and dp2, and 5.8mm between dp2 and p3. Considerable variation occurred between the sizes of the diastemata in both jaws of all adults examined.

We suggest that the presence, absence and size of diastemata between premolars should be used with caution in assessing the phylogenetic relationships among fossil thylacinids, especially when only one or two specimens are known for any fossil species.

Another comment refers to the continued use of the terms P1 and P2 in the adult jaws of fossil and extant thylacinids, and in other marsupials in general. In all marsupials that have been examined histologically from early developmental stages up to the eruption of all teeth, there is no evidence known to us for the replacement of dP1 or dP2 by a successor P1 or P2 in the upper or lower jaws of any fossil or extant marsupial. This has been emphasised previously for both fossil (Cifelli et al., 1996) and extant (Luckett, 1993a, b; Luckett and Woolley, 1996) marsupials. Authors who continue to use the terms "P1 and P2" should present evidence for the replacement of their deciduous predecessors in marsupials, as is the case for dP3 and P3. Similar usage of the term "P1" instead of dP1 within fossil and extant eutherians has been discussed recently in a study on Eocene juvenile perissodactyls (Rose et al., 2018).

A final, very positive, observation on thylacine biology and evolution. We were pleased to see the publication on development of the immune system (Old, 2015) in the pouch young of *Thylacinus* that was based on the histological sections of NMV C 5754 from Museums Victoria. Hopefully, other investigators will study additional aspects of the cranial and postcranial biology in this specimen. We are also happy to note the recent publication of the thylacine genome (Feigin et al., 2018), thanks to the use of material from the sister (NMV C 5757) of our sectioned pouch young in the Museums Victoria collection (see fig. 2b).

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Taxonomic revision of dragon lizards in the genus *Diporiphora* (Reptilia: Agamidae) from the Australian monsoonal tropics

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Abstract

Melville, J., Smith Date, K.L., Horner, P., and Doughty, P. 2019. Taxonomic revision of dragon lizards in the genus *Diporiphora* (Reptilia: Agamidae) from the Australian monsoonal tropics. *Memoirs of Museum Victoria* 78: 23–55.

The Australian dragon lizard genus *Diporiphora* currently comprises 21 species based on genetic and morphological evidence, with 11 of these species occurring in the monsoonal tropics of northern Australia. *Diporiphora* are climbing lizards that are found on either trees, grasses or rocks, with usually only subtle morphological differences to distinguish between species. Since the last taxonomic treatment of this genus in northern Australia over 40 years ago, species delimitation using genetic techniques has clarified the number of lineages and increased collections from recent surveys have significantly broadened the distributions of these taxa. However, no formal taxonomic assessments have been undertaken to redefine species, including the many lineages that represent undescribed species. Currently, there are seven species of *Diporiphora* with vast distributions across northern Australia and a broad and variable set of morphological characteristics that make species identification challenging, even for experienced field workers. Here, we provide a comprehensive taxonomic treatment of *Diporiphora* species across northern Australia based on previously published genetic data and morphological examination of voucher specimens. Our analyses demonstrate that these broadly distributed taxa actually comprise multiple, often allopatric, species, with especially high diversity in the Kimberley region of Western Australia.

We redescribe nine previously described species and describe five new species of *Diporiphora* based on historical types, newly collected material and older museum vouchers. In the *D. australis* species group, we resurrect *D. jugularis* Macleay from synonomy. In the *D. bennettii* species group, we synonomise *D. arnhemica* Storr with *D. albilabris* Storr, and raise to full species the latter and *D. sobria* Storr. In addition, we describe as new a wide-ranging saxicoline species previously attributed to *D. bennettii* Gray. In the *D. bilineata* species group, we resurrect *D. margaretae* Storr from synonomy with *D. magna* Storr and describe three new species. Lastly, we describe a species from the northwest Kimberley that is more closely related to an arid zone radiation.

The revision of the northern *Diporiphora* dragons here stabilises the taxonomy, redefines many species distributions and reveals many new species. Further work on *Diporiphora* includes further surveys to better understand distributions and habitat preferences and continue to refine their evolutionary history and biogeography in northern Australia.

Keywords

Agamid lizards; Australia; Cape York Peninsula; *Diporiphora carpentariensis* sp. nov.; *Diporiphora gracilis* sp. nov.; *Diporiphora granulifera* sp. nov.; *Diporiphora pallida* sp. nov.; *Diporiphora perplexa* sp. nov.; Kimberley; monsoonal tropics; taxonomy; Top End.

Introduction

The Australian monsoonal tropics (AMT) constitute a significant element of the Australian landmass, spanning the northern quarter of the continent from the far west coast of the Kimberley region in Western Australia (WA), across the Top End of the Northern Territory (NT) and around the Gulf of Carpentaria to the Cape York Peninsula in Queensland. Tropical savannah woodlands and grasslands are the region's dominant vegetation types and are characterised by a dense grass understorey and an over-storey of widely scattered trees (Bowman et al., 2010). These woodlands are home to a major component of Australian biodiversity, with sandstone escarpments possibly having similar levels of diversity to the rainforests (Bowman et al., 2010). Despite the importance and size of this region in terms of phylogenetic diversity, there are many vertebrate groups for which there remain significant

taxonomic problems, particularly in terms of under-representing the true species diversity (e.g. Doughty 2011; Laver et al., 2018; Moritz et al., 2018; Pepper et al., 2011).

One group with such taxonomic problems is the dragon lizard genus *Diporiphora* (family Agamidae, sub-family Amphibolurinae), which is a diverse group of slender small-bodied dragons, including some of the most common and widespread diurnal lizards across the tropical savannah woodlands. This genus presents particular difficulties in species-level identification, with many of the morphological characters used in keys and diagnoses being as variable within species as between species. The last significant taxonomic treatment of *Diporiphora* in this region of northern Australia was published more than 40 years ago, describing eight species and subspecies (Storr, 1974). More recently, genetic work has shown that the current taxonomy significant under-represents the true species diversity (Couper et al., 2012; Edwards and Melville, 2011; Smith et al., 2011).

We undertook a comprehensive taxonomic review of *Diporiphora* species across northern Australia, with particular focus on the taxa that have been identified as species complexes in previously published and unpublished genetic work (fig. 1). Although Storr's (1974) work provides a good framework towards resolving the taxonomy of northern *Diporiphora*, many issues remain. As was typical of Storr's work, his revision was based on collections at the Western Australian Museum (WAM); he did not address Queensland, despite *Diporiphora* occurring across the Gulf of Carpentaria region including the Cape York Peninsula.

Storr (1974) recognised considerable diversity within several species and described multiple subspecies to accommodate this variation: *D. albilaris* (*D. a. albilaris, D. a. sobria*), *D. bennettii* (*D. b. bennettii, D. b. arnhemica*) and *D.*

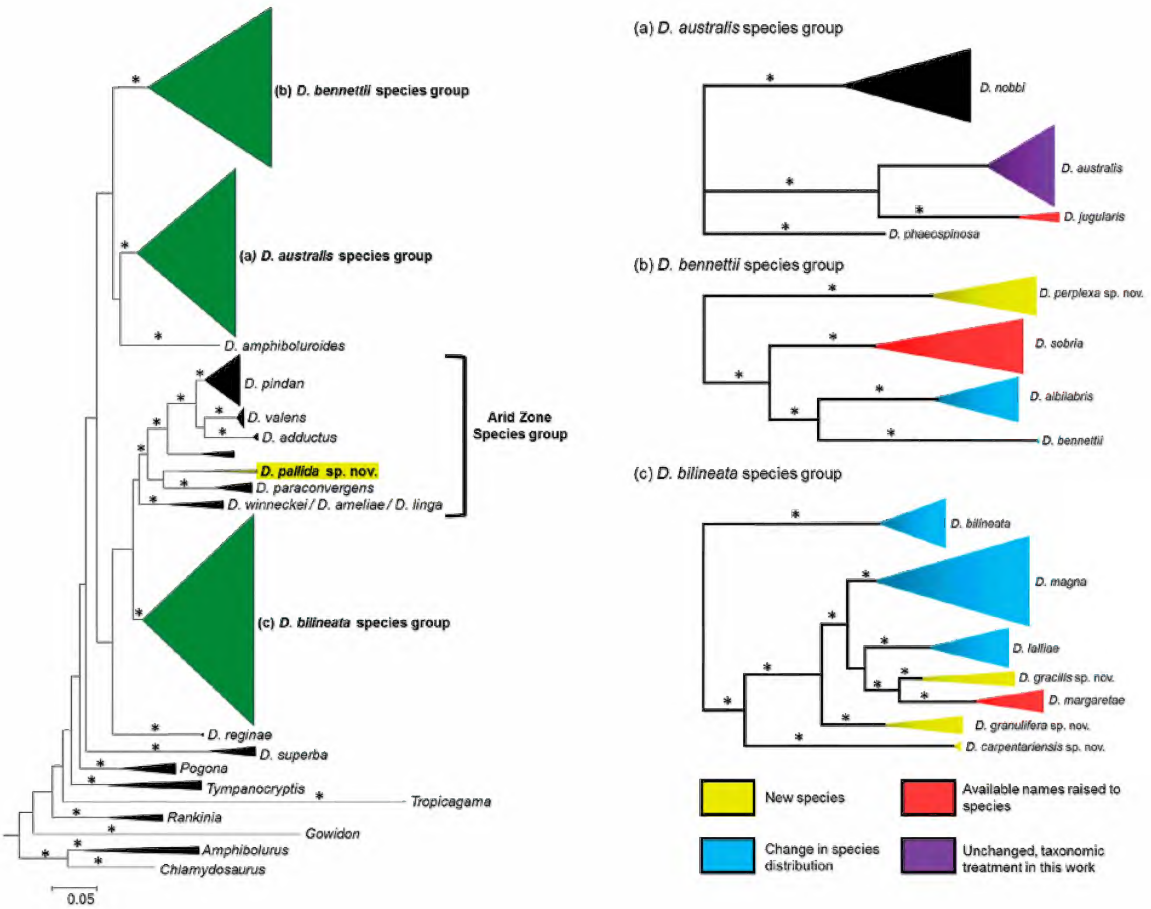

Figure 1. Bayesian 50% majority-rules phylogenetic tree for *Diporiphora* based on mtDNA on ~1200 bp mitochondrial DNA (ND2). Asterisks on branches represent >99% posterior probability support. Clades highlighted in green are expanded, with phylogenetic relationships within each of the species groups reviewed in the current paper: a, *D. australis*; b, *D. bennettii*; c, *D. bilineata*. Species reviewed in the current paper are coloured to represent the taxonomic revision that is undertaken.

Table 1. Meristic characters scored and morphological characters measured in this study

Meristic characters	
Pre-cloacal pores	Number of pre-cloacal pores in total
Femoral pores	Number of femoral pores in total
Canine teeth	Number of canine teeth on each side of upper jaw
Guar fold	Absent/weak/present
Post-auricular fold	Absent/weak/present/strong
Scapular fold	Absent/weak/ present/strong
Dorsal scales	Homogenous/weakly heterogeneous/strongly heterogeneous
Throat stripes	Absent/weak/strong
Position of lateral dark spot	On side of neck/axilla (arm pit)
Paravertebral and dorsolateral scales	Enlarged or homogenous with surrounding scales
Vertebral scales	Enlarged or homogenous with surrounding scales
4th toe lamellae (4TL)	Number of enlarged subdigital lamellae under fourth toe, counted from toe junction to base of claw
Infralabials (ILB)	Number of infralabial scales, ending with the last small scale in contact with the posterior margin of the last upper labial
Supralabials (SLB)	Number of supralabial scales
Measurements	
SVL	Snout-vent length
Tail (TL)	Tail length from cloaca to tip (unbroken tails only)
Head length (HL)	Head length, measured obliquely from tip of snout to anterior margin of tympanum
Head width (HW)	Head width, measured at the widest point
Interlimb length (IL)	Length from the axilla to the groin
Forelimb (FLL)	Length, measured from the elbow bend to the tip of the 4th finger including claw
Hindlimb (HLL)	Length, measured from the knee bend to the tip of the 4th toe including claw

bilineata (*D. b. bilineata, D. b. margaretae*). At the time of Storr's revision, subspecies were fashionable to employ to deal with the variation observed and to hedge against taxonomic uncertainty, especially with the relatively small number of specimens he had to work with. Since Storr's revision, the concept of these species has changed according to various authors and field guides but without any formal taxonomic treatment. For example, the subspecies *D. b. arnhemica* is usually recognised as a full species (e.g. Cogger et al., 2014; Wilson and Swan, 2017). Additionally, the distributions of these subspecies have significantly expanded since Storr's (1974) original descriptions. For example, *D. b. arnhemica* was originally limited to the type location, *D. a. sobria* was limited to two locations in the central NT and *D. a. albilabris* was limited to four locations in the northwest Kimberley. Subsequently, the distributions of these taxa have expanded to encompass vast areas of northern Australia (e.g. Cogger, 2014; Wilson and Swan, 2017).

Taxonomic problems, such as those outlined above, extend across all northern *Diporiphora* species. Storr (1974) described *D. b. margaretae* as a new subspecies of *D. bilineata,* with distributions of the two subspecies (*D. b. bilineata* and *D. b. margaretae*) defined as being disjunct in the NT and northern Kimberley, respectively, with the intervening savannah woodlands occupied by *D. magna* (also described in the same work). Finally, *D. lalliae* was described as a generalist species with a broad east–west distribution across the southern portions of the AMT (Storr, 1974). Since the description of these species and subspecies, many of the distributions of these lineages have expanded to be widespread and broadly sympatric across the AMT and even into the arid zone (*D. lalliae*) without further taxonomic treatment. Storr apparently changed his mind about the legitimacy of *D. b. margaretae*, omitting it from Storr et al. (1983) without comment 10 years later. This change has been largely followed since (e.g. Cogger, 2014; Wilson and Swan, 2017) despite being listed as a full species by Cogger et al. (1983). Thus, the currently used taxonomy of northern Australian *Diporiphora* does not reflect Storr's original work and a full taxonomic assessment of these lizards is long overdue.

Table 2. Diagnostic characters to distinguish between lineages

		(a) *D. australis* species group	(b) *D. bennettii* species group	(c) *D. bilineata* species group	(d) Arid zone species group
1.	No. of canine teeth on each side of upper jaw	One	Two	One	One
2.	Axilla granular scales	Absent	Absent	Present Exception: absent in *D. lalliae*	Absent
3.	Lateral dark spot	On side of neck	Axial if present	Axial	Absent
4.	Femoral pores	Absent	Present (*D. albilabris*, *D. sobria*) or absent	Absent	Absent

Here, we provide the first comprehensive taxonomic treatment of *Diporiphora* species across northern Australia since Storr's work, using an understanding of relationships based on genetic data and an examination of newly collected and historical collections, including type specimens.

Methods

Specimens examined and external morphology

Specimens were examined from the collections of the Western Australian Museum (WAM), Queensland Museum, Brisbane (QM), Museum Victoria (NMV), Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, Australia Museum, Sydney (AMS), the Natural History Museum, London (NHMUK, registration prefix – BMNH), the Naturhistorisches Museum, Vienna (NHMW) and the Swedish Museum of Natural History (NHRM). New type material is deposited in the WAM and QM.

A set of 13 meristic and seven morphometric characters (Table 1) were recorded for all primary types. Measurements were made with electronic callipers to the nearest 0.1 mm, except for snout-vent length (SVL) and tail length (broken tails were not measured), which were measured with a ruler to the nearest 0.5 mm. Individuals were sexed by observations of everted hemipenes in males or heavily gravid females, or by direct examination of the gonads. Aside from the type series, an additional ≥10 well-preserved adult specimens (where available) from each taxon were examined (listed in Appendix 1). On the dorsum, we refer to the vertebral scale row at the midline, with the paravertebral scale row adjacent and with the 2nd paravertebral scale row (often enlarged and hence referred to in the text) to the outside of the paravertebral row. We detail both meristic and morphological characters to diagnose species and to identify the species groups from each other. In the *Comparisons with other species* sections, we compare the focal species with other species that have overlapping distributions.

We provide a taxonomic revision of each of the species groups outlined in fig. 1. This encompasses most of the *Diporiphora* that occur across the AMT and a species description for a taxon that falls outside these species groups but occurs within the AMT:

(a) *D. australis* species group
(b) *D. bennettii* species group
(c) *D. bilineata* species group
(d) arid zone species group.

Five *Diporiphora* species that occur in the northern tropical savannahs are not reviewed in the current study. *Diporiphora superba* Storr is extremely elongate and green or yellow, and is easily distinguished from all other Australian dragon lizards (Storr et al., 1983; Wilson and Swan, 2017). The type of *D. convergens* Storr was examined as part of this study but an account is not included because this specimen has the keels of the dorsal scales converging towards the midline, which is unique in AMT *Diporiphora*. This species is only known from the type specimen, which was collected from Crystal Creek in the northern tip of the Kimberley (Storr, 1974) and has not been collected again. Taxonomic treatments of *D. nobbi* (Witten), *D. phaeospinosa* Edwards and Melville or *D. pindan* Storr are also not provided because they have been recently treated elsewhere (Doughty et al., 2012a; Edwards and Melville, 2011).

Phylogenetic analyses

The phylogenetic tree (fig. 1), based on a region of ~1200 bp mtDNA (including the protein coding gene ND2 and five tRNAs) across 283 *Diporiphora* samples, provides strong support for all lineages covered in this taxonomic review. The ND2 coding region and flanking tRNA regions were found to follow the GTR+I+G model of substitution with no partitioning schemes using the corrected Akaike information criterion on PartitionFinder2 on the CIPRES Science Gateway (Lanfear et al., 2016). Bayesian analysis was performed using MrBayes (Huelsenbeck and Ronquist, 2001) on the CIPRES Science Gateway, with two runs of four independent Markov chain Monte Carlo analyses (each 50,000,000 generations long and sampled every 1,000 generations) under a GTR+I+G model with flat priors. Tracer v1.6 was used to check for stationarity and convergence of the chain outputs. The trees were subject to a 25% burn-in in MrBayes, summarised and posterior probabilities obtained.

Diporiphora Gray, 1842

Type species. *Diporiphora bilineata* Gray, 1842, by monotypy.

A diverse genus, distributed across all states and territories, except Tasmania, predominately in semi-arid, arid and AMT biomes. Small- to medium-sized lizards that are mostly terrestrial or semi-arboreal. Moderately long snout with relatively long legs and tail. All species have exposed tympanum, and most species have pre-cloacal pores with femoral pores occasionally present. Generally lacking prominent crests, large spinose scales or dermal appendages, although present in some species (e.g. *D. amphiboluroides*). Colour patterning variable within species, particularly between breeding males and females or juveniles. In general, most species have pale dorsolateral stripes, dark transverse dorsal bars, a black circular blotch on shoulders or neck, and a pink to mauve flush on hips and tail base (particularly in adult males).

(a) *D. australis* species group (fig. 1a)

Content:

Diporiphora australis (Steindachner, 1867)
Diporiphora jugularis (Macleay, 1877)
Diporiphora nobbi (Witten, 1972)
Diporiphora phaeospinosa Edwards and Melville, 2011

Diagnostic characters for group (Table 2):

- one canine tooth on each side of upper jaw (see fig. 2 for illustration of this character)
- scales in axillary region not granular
- lateral dark spot on side of neck.

Remarks

This species group is restricted to the eastern portion of the AMT (fig. 3), occurring along the east coast, adjacent inland areas and throughout the Cape York Peninsula. Relative to other species groups in the AMT, they tend to be large bodied (68–75 mm SVL) with generalist habits. We do not include *D. nobbi* and *D. phaeospinosa* below because Edwards and Melville (2011) recently reviewed these species. Our analyses of all *Diporiphora* species (fig. 1a) recovered the same relationships among species within this group as the mtDNA phylogeny in Edwards and Melville (2011), with *D. australis* and *D. jugularis* being highly supported as sister species, but the relationships between this lineage and *D. phaeospinosa* and *D. nobbi* are not well resolved. We provide an account of *D. australis* and *D. jugularis*, raising the latter species from a junior synonym of *D. bilineata* (Cogger et al., 1983) based on genetic results in Edwards and Melville (2011) and examination of types and specimens herein.

Diporiphora australis (Steindachner, 1867)

Common name. Tommy roundhead.

Figure 4, Tables 3, 4

Calotella australis Steindachner, F. 1867. Reptilien. pp. 1–98 in, *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologie* 1(3). State Printer: Vienna. [1869 on title page] [29, pl. 1 fig. 9]. Type data: lectotype – NHMW 19821.1 Australia ("Cape York, QLD" on type label), taxonomic designation, this work.

Grammatophora macrolepis Günther, A. 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20: 45–68 [51]. Type data: holotype – BMNH 1946.8.12.74, Australia (by implication).

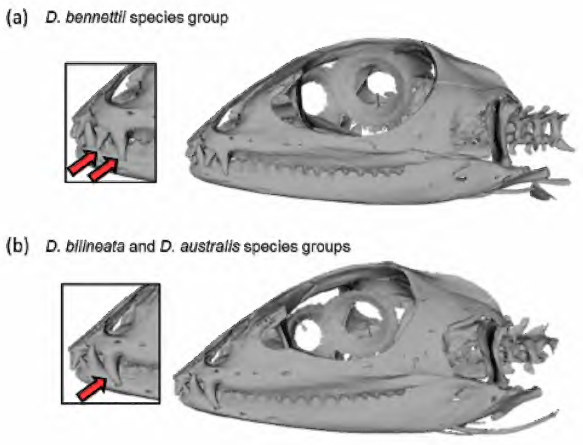

Figure 2. Images from micro X-ray computed tomography scans showing the differences in pleurodont (canine) tooth number in the upper jaw: a, arrangement in *D. bennettii* species group; b, other species groups included in the current study.

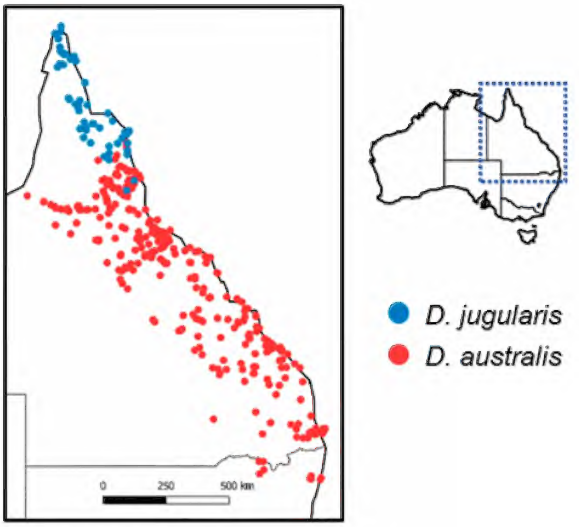

Figure 3. Distributions of *D. australis* and *D. jugularis* based on specimens examined and collection records.

Table 3. Measurements and sex of types. All measurements are in millimetres (mm) and key to abbreviations can be found in Table 1. Museum abbreviations are as follows: Western Australian Museum (WAM); Australian Museum, Sydney (AMS); Queensland Museum (QM); Natural History Museum, United Kingdom (BMNH); Naturhistorisches Museum, Vienna, Austria (NHMW)

Species	Accession No.	Sex	SVL	TL	HL	HW	IL	HLL	FLL	4TL	SLB	ILB
D. australis	NHMW 19821:1	female	69	146	18	12	33	49	27	23	11	12
D. jugularis	AMS R40672	juvenile	38	96	12	7	16	35	22	23	11	12
D. jugularis	AMS R40673	juvenile	35	82	12	8	16	34	22	23	11	12
D. jugularis	AMS R40674	juvenile	30	65	11	8	16	30	19	22	10	11
D. bennettii	BMNH 1946.8.12.77	female	50	68	15	13	24	36	23	17	11	10
D. albilabris	WAM R43517	female	44	94	14	9	20	40	24	18	10	10
D. sobria	WAM R23180	subadult	34	68	12	8	14	25	19	18	11	12
D. perplexa sp. nov.	WAM R177290	male	63	140	22	11	24	52	31	21	11	11
D. bilineata	BMNH 1946.8.12.75	male	58	56*	18	13	24	46	26	23	11	10
D. bilineata	BMNH 1946.8.12.76	male	57	131	17	12	24	42	24	22	10	11
D. lalliae	WAM R23020	male	62	152	18	11	34	44	27	23	9	9
D. magna	WAM R42786	female	47	141	15	9	20	42	25	23	11	11
D. margaretae	WAM R27648	female (gravid)	55	128	16	9	24	41	27	19	11	13
D. gracilis sp. nov.	WAM R177291	male	57	165	18	10	20	49	27	23	11	9
D. granulifera sp. nov.	QM J96362	male	65	176	21	12	29	46	31	23	11	12
D. carpentariensis sp. nov.	QM J88197	male	62	185	20	12	28	55	33	22	11	11
D. pallida sp. nov.	WAM R177292	male	46	95	15	10	24	40	24	16	10	11

* = tail broken

Diporiphora nuchalis De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [98]. Type data: syntype(s) – whereabouts unknown, central and south-coast district, Queensland.

Diporiphora ornata De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, locality unknown.

Physignathus nigricollis Lönnberg, E., and Andersson, L.G. 1915. Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913. VII. Reptiles collected in northern Queensland. *Kongliga Svenska Vetenskaps-Academiens Nya Handlingar, Stockholm* 52: 1–9 [4] [incorrect spelling as *Physignatus nigricollis*]. Type data: holotype – NHRM 3209, Cooktown, Queensland.

Diagnosis. Body size moderately large (to 70 mm SVL) with long tail (2.3–2.7 × SVL). Gular, post-auricular and scapular folds present. Lacks spinose scales on thighs or neck. Precloacal pores 4; femoral pores 0.

Description of lectotype. Female; 69 mm SVL; 146 mm tail length. Medium-sized dragon, moderately robust with moderately long limbs and tail. Single canines on each side of upper jaw. Gular and post-auricular folds present and scapular fold weak. Dorsal scales homogenous but prominent keels form longitudinal ridges along dorsum along midline with dorsolateral ridges on each side; these raised vertebral and dorsolateral scale rows extend anteriorly onto nape to head and posteriorly onto base of tail, not extending down tail. Scales on flanks heterogeneous with scattered slightly enlarged scales. Scales on neck, limbs and tail not spinose. Scales in axilla small but not granular. Ventral scales strongly keeled. Precloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Vertebral and dorsolateral lines very faint, almost undiscernible with colouring a slightly paler replication of dorsum patterning, running from back of head to pelvis. Five wide dark transverse bands across dorsum between head and pelvis. Dark bands are a similar width to the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Lacks dark spot on posterior of tympanum. Flanks a similar colour to dorsum. Lacks lateral stripe between axilla and groin. Dark patch on sides of neck at anterior edge of shoulder. Arms weakly banded with dark bands slightly narrower than light. Legs and tail strongly banded with dark bands narrower than light. Ventral surface cream with no patterning.

Variation. 46–70 mm SVL; 105–174 mm tail length. Tail long, ranging from 2.3–2.7 × SVL. Strong scapular fold present, post-auricular fold usually absent although present but weak in a few individuals. Dorsal scales homogenous but prominent keels form longitudinal ridges. There are often five longitudinal ridges: one along the vertebral midline, one each on the 2nd paravertebral scale rows and one on each of the dorsolateral stripes. Some individuals only have these longitudinal ridges running along the

Table 4. Diagnostic characters distinguishing species within species groups

	Tail length (× SVL)	Dorsolateral stripes	Gular fold	Post-auricular fold	Scapular fold	Dark spot on tympanum edge	Extent of axial dark granular scales	Dorsal scales between dorsolateral stripes	Pre-cloacal pores (total)	Femoral pores (total)
(a) *D. australis* species group										
D. australis	Long (2.3–2.7)	Present	Present	Weak/ absent	Present	Absent	Absent	Homogeneous	4	0
D. jugularis	Long (1.8–2.7)	Usually	Absent	Absent	Absent	Absent	Absent	Homogeneous	4	0
(b) *D. bennettii* species group										
D. albilabris	Long (1.8–2.5)	Present	Present	Strong	Absent	Absent	Absent	Strongly heterogeneous	4	2
D. bennettii	Short (<2.0)	Absent	Present	Strong	Weak	Absent/ weak	Absent	Homogeneous	2	0
D. perplexa sp. nov.	Long (1.9–2.5)	Present	Weak	Strong	Weak	Strong	Absent	Homogeneous	2–4	0
D. sobria	Long (2.3–2.6)	Present	Present	Weak/ present	Weak/ present	Absent/ weak	Absent	Homogeneous in Western Australia (some Northern Territory populations heterogeneous)	4	2
(c) *D. bilineata* species group										
D. bilineata	Long (2.2–2.7)	Present	Absent	Absent	Present	Absent	Over arm onto shoulder and posteriorly along flanks, with pale flecks	Moderately heterogeneous with outer row of dorsolateral stripe having weakly raised trailing edge	2	0
D. gracilis sp. nov.	Very long (2.7–3.0)	Sometimes	Absent	Weak/ absent	Weak	Absent	Over arm to scapular fold	Homogeneous lacking raised scales in dorsolateral stripes	4	0
D. lalliae	Very long (2.7–3.4)	Usually	Present	Strong	Strong	Absent	Absent	Homogeneous lacking raised scales in dorsolateral stripes	4	0
D. magna	Very long (2.6–3.0)	Present	Absent	Strong	Strong	Absent	Over arm but not to sides of neck	Homogeneous lacking raised scales in dorsolateral stripes	4	0
D. margaretae	Long (2.5–2.7)	Present	Absent	Weak/ present	Weak/ present	Absent	On top of arm and posteriorly along flanks, with pale flecks	Homogeneous but with outer row of dorsolateral stripe having raised trailing edge	4	0
D. granulifera sp. nov.	Very long (2.7–3.0)	Present	Absent	Weak–strong	Strong	Absent	Over arm and along the full length of the scapular fold; anterior to scapular fold small, slightly granular scales	Homogeneous but with outer row of dorsolateral stripe having raised trailing edge	4–6 (usually 4)	0

	Tail length (× SVL)	Dorsolateral stripes	Gular fold	Post-auricular fold	Scapular fold	Dark spot on tympanum edge	Extent of axial dark granular scales	Dorsal scales between dorsolateral stripes	Pre-cloacal pores (total)	Femoral pores (total)
D. carpentariensis sp. nov.	Very long (2.1–3.0)	Present	Absent	Weak–strong	Strong	Absent	Over arm and along the full length of the scapular fold	Homogeneous lacking raised scales in dorsolateral stripes	4–5 (usually 4)	0
(d) Arid zone species group										
D. pallida sp. nov.	Short (2.0)	Absent	Present	Absent	Present	Absent	Absent	Homogeneous	2	0

second scales out from the midline, giving a smoother appearance to the dorsum. Some individuals have weakly heterogeneous dorsal scales with the 2nd paravertebral scale rows slightly enlarged. In individuals with weak post-auricular fold, a row of 4–6 enlarged but not spinose scales may be present.

Dorsal pattern variable from strong, complex patterning to unpatterned. Dorsolateral stripes always present, wide cream to grey vertebral stripe present in all but weakly patterned individuals. In strongly patterned individuals, usually six dark transverse bands across dorsum between head and pelvis but ranges from 4–7. Transverse bands similar in size or slightly narrower than pale background. Flanks in these individuals have similar patterning to dorsum and commonly have wide pale lateral stripe between axilla and groin. In weakly patterned individuals, transverse bands are either absent or are narrow dark bands contacting the dorsolateral stripes and extending towards, but not contacting, the vertebral stripe. In these plain animals, the bands on the tail also contact the dorsolateral stripes but do not meet at the midline. Flanks in these individuals lack patterning, including a lateral stripe between axilla and groin. Dark patch on sides of neck often present but variable from being absent to running along scapular fold and extending anteriorly onto the sides of neck from the dorsal extent of the fold, with the dark pigmentation contacting the pale dorsolateral stripe. This dark spot on the neck never extends posteriorly from the scapular fold towards the axial region or onto the ventral surface. Ventral surface usually unpatterned and cream in colour, but a few individuals, usually females, have pale grey colouring on gular region.

Distribution and ecology. Widespread along the north-eastern coast of Australia, as far south as the Coffs Harbour area in northern New South Wales, extending north along the coast into the south-eastern portions of Cape York Peninsula as far north as the Cooktown area (fig. 3). It extends inland approximately 600 km from the coast, across the base of Cape York Peninsula to the Normanton area. It extends south along the Great Dividing Range, into northern New South Wales.

A common and abundant species that is an ecological generalist, occurring in most dry forests and woodlands within its distribution (fig. 5c and e). Individuals use low vegetation, fallen timber and termite mounds as perches. This species is a common sight in some of the northern cities and appears to have adapted well to bushy suburban areas (Kutt et al., 2011). Although *D. australis* is one of the most common species encountered in suburban areas of eastern Queensland, relatively little is known about its biology.

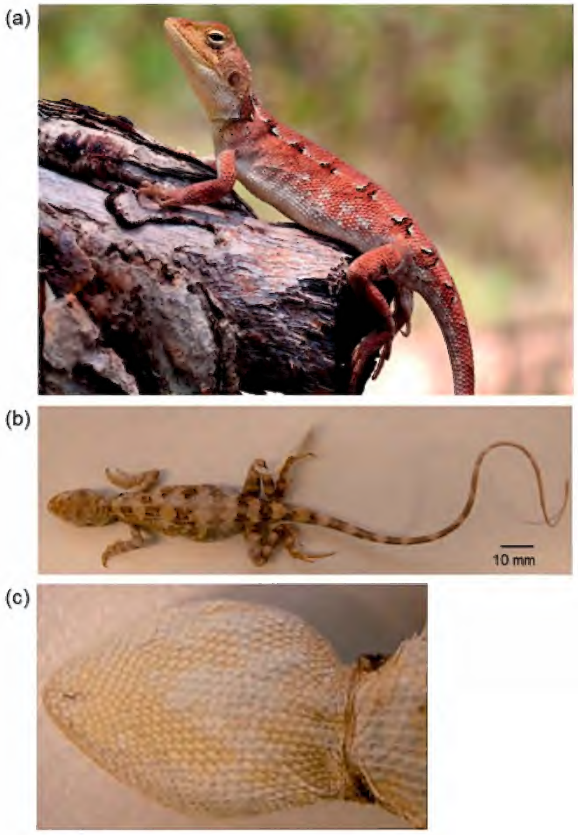

Figure 4. *Diporiphora australis*: a, adult, Karawatha, south-eastern Queensland (photo: S. Wilson); b, lectotype NHMW 19821.1, Australia ("Cape York, QLD" on type label); c, ventral view of head showing gular fold.

Comparison with other species. Overlaps extensively with the distribution of *D. nobbi* and overlaps broadly with *D. jugularis* at the northern edge of its range (fig. 3) and with *D. carpentariensis* sp. nov. in the north-western extent of its range. It differs from *D. nobbi* in having smaller body size and lacking spinose scales on the thighs or neck. It can be distinguished morphologically from *D. jugularis* and *D. carpentariensis* sp. nov. by possessing a gular fold.

Remarks. As part of this study we examined all available types, including those of synonymised species, held in Australian and European collections. In addition, we examined a specimen

Figure 5. Examples of the range of habitats in which the *Diporiphora* species of the Australian monsoon tropics occur: a, sandstone escarpment, Mitchell Plateau, Kimberley region, Western Australia; b, rocky outcrops in savannah woodlands, western Arnhem Land, Northern Territory; c, savannah woodlands, Kimberley region, Western Australia; d, savannah grasslands on cracking clay soils, floodplain of the Lennard River, Kimberley Region, Western Australia; e, savannah woodlands, western Arnhem Land, Northern Territory; f, arid spinifex grasses with scattered trees on stony ground, Tennant Creek, Northern Territory (photos: J. Melville).

held in the NHMUK that is housed in the type collection based on an account by Günther (1867). This account named *Grammatophora calotella* as a replacement name for a species described earlier in the same year by Steindachner, who described *Calotella australis*, basing his name on specimens in the Vienna collection. Günther renamed *Calotella australis* as the species *Grammatophora calotella* and referred to the two specimens in the NHMUK from Cape York. However, examination of the *Grammatophora calotella* specimen revealed that it lacks a gular fold, indicating that it is *D. jugularis* from Cape York, and not *C. australis*. In the same paper, Günther described *Grammatophora macrolepis* as a new species, which examination confirms is *D. australis*.

Cogger et al. (1983) suggested that the two specimens with the single registration number of NHMW 19821 were likely to be the syntypes and that these bore the locality "Cape York", suggesting that they were collected by Daemel. As such, they would have been collected by Daemel at the same time as the *Grammatophora calotella* specimens in the NHMUK (BMNH 66.12.28.22–23). However, it is probable that the location of these specimens is incorrect and they were not from Cape York but were from Rockhampton. Comparison of the lectotype NHMW19821:1 to the image provided in the original description (fig. 6) suggests that this specimen was the one described by Steindachner but with incorrect locality data. There are several species with types collected by Daemel where there is a mix-up between specimens collected in Cape York and Rockhampton (G. Shea, personal communication).

The type of *Physignathus nigricollis* Lönnberg and Andersson was also examined as part of this study and was confirmed to be a specimen of *D. australis*.

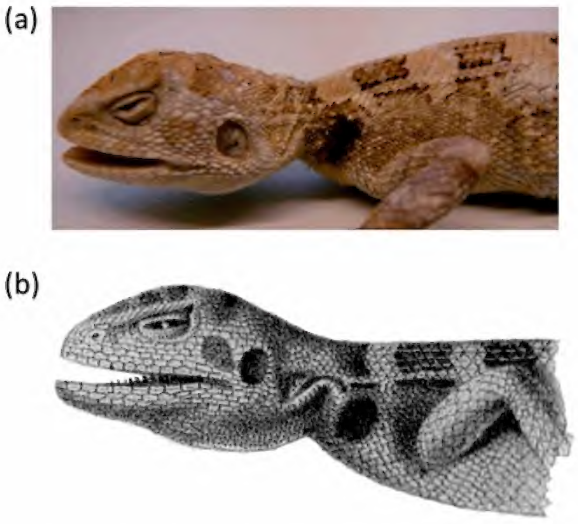

Figure 6. Lateral images of the *Diporiphora australis* syntype NHMW 19821:1: a, Naturhistorisches Museum, Vienna (photo: J. Melville); b, taken from the original species description (Steindachner, 1867).

***Diporiphora jugularis* (Macleay, 1877)**

Common name. Black-throated two-pored dragon.

Figure 7, Tables 3, 4

Grammatophora jugularis Macleay, W. 1877. The lizards of the Chevert Expedition. Second paper. *Proceedings of the Linnean Society of New South Wales* 2: 97–104 [1878 on title page] [104]. Type data: syntype(s) – AMS R40672–4, Cape Grenville, Cape York Peninsula, Queensland.

Diporiphora brevicauda De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, Cape York Peninsula, Queensland.

Diporiphora pentalineata De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, Cape York Peninsula, Queensland.

Diagnosis. Body size moderately large (to 68 mm SVL) with long tail (1.8–2.7 × SVL). Gular and scapular folds absent; post-auricular fold absent or weak. Scales in axilla not granular. Lacks spinose scales on thighs or neck. Pre-cloacal pores 4; femoral pores 0.

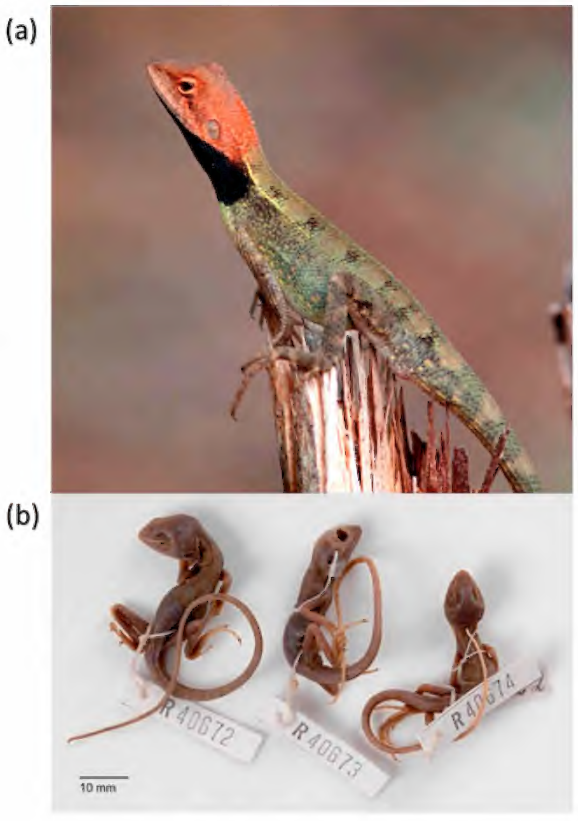

Figure 7. *Diporiphora jugularis*: a, adult male with breeding colouration, Iron Range, Queensland (photo: S. Wilson); b, syntype(s) AMS R40672–4, juveniles, Cape Grenville, Cape York Peninsula, Queensland.

Description of syntypes. Juveniles; 30–38 mm SVL; 65–96 mm tail lengths. Small dragons, moderately robust with moderately long limbs and tail. Single canines on each side of upper jaw. Gular, scapular and post-auricular folds absent. Dorsal scales homogenous but raised keels form four prominent longitudinal ridges along dorsum, with a ridge on either side of midline running along the 2nd paravertebral scale row, and a dorsolateral ridge on along each side. These raised vertebral and dorsolateral scale rows extend anteriorly to neck, terminating at head and extending posteriorly onto base of tail. Scales on flanks strongly heterogeneous with scattered scales that are distinctly larger than rest, with keels angling away from dorsum towards ventral surface from midbody. Scales on neck, limbs and tail not spinose. Scales in axilla small but not granular. Ventral scales strongly keeled, keels forming longitudinal ridges running length of body. No pre-cloacal pores visible in these juvenile specimens (usually 4); femoral pores 0.

Dorsum not patterned, which may be due to preservation. Lack vertebral and dorsolateral lines. Dark transverse bands across dorsum absent. Heads plain without patterning, labials same colour to rest of head and lacking pale line between eye and ear. Lacking dark spot on posterior of tympanum. Flanks same colour as dorsum. No lateral stripe between axilla and groin. Faint dark pigmented patch on either side of neck at anterior edge of shoulder. Arms, legs and tail plain. Ventral surface cream with no patterning.

Variation. 54–68 mm SVL; 99–178 mm tail length. Tail long, ranging from 1.8–2.7 × SVL. Gular, scapular and post-auricular folds absent in all individuals examined. Dorsal scales homogenous but prominent keels form longitudinal ridges. There are often five longitudinal ridges: one along the vertebral midline, one on either side midline running along the 2nd paravertebral scale row and one on each of the dorsolateral stripes. However, some individuals only have these longitudinal ridges running along the 2nd paravertebral scale row, giving a smoother appearance to the dorsum. Weakly heterogeneous scales in some individuals, with the scale rows second out from the midline being slightly enlarged. Spinose scales absent, but some individuals have 4–6 enlarged (not spinose) scales where a post-auricular fold would occur. Pre-cloacal pores 4; femoral pores 0.

Dorsal patterning variable from plain to strongly patterned. Adult males often have little patterning, but with strongly keeled dorsolateral ridge of scales with a pale cream colour forming prominent dorsolateral stripes. Flanks on these individuals are dark brown with the scattered enlarged pale brown or cream scales giving a speckled or flecked appearance, lacking lateral stripe. Patterned individuals, typically adult females and juveniles, have approximately 4–7 broken dark transverse bands across dorsum on a pale background. Dark bands are of similar width or slightly broader than pale background. These bands are broken by a pale grey or light brown vertebral stripe. The dark transverse bands continue laterally beyond the pale cream dorsolateral stripes, becoming diffuse and terminating at a poorly defined lateral stripe. Wide dark band on sides of neck mostly present, extending from the dorsolateral stripe to the gular ventral surface and anteriorly from where a post-auricular fold would be to the anterior of the shoulder. The dark band is prominent in males and smaller or occasionally absent in females. This dark gular band does not extend onto chest but forms a well-defined posterior edge across the gular region. In adult males, the dark gular band extends anteriorly to the labials, while in individuals with smaller gular bands, the apex of the small central triangle extends anteriorly. Individuals without the dark gular band may have a dark spot on either side of the neck or a narrow grey band across gular. Legs and tail banded in strongly patterned individuals, otherwise little patterning on legs and tail.

Distribution and ecology. Restricted to the eastern edge of the Cape York Peninsula, extending as far south as Mount Misery, southwest of Cairns (fig. 3). Widespread along the eastern extent of Cape York Peninsula, extending inland 150 km from the coast. Little is known about the ecology of this species, but presumed to be similar to that of its sister species *D. australis* in the NT. If so, it would be a generalist species that occurs in dry open forests, woodlands and shrublands.

Comparison with other species. Overlaps geographically with *D. australis*, *D. nobbi* and *D. carpentariensis* sp. nov. It differs morphologically from both *D. australis* and *D. nobbi* in lacking a gular fold. Also differs from *D. nobbi* in being smaller in body size (65 mm vs. 75 mm SVL), lacking spinose scales on the thighs or neck, having fewer pre-cloacal pores and lacking femoral pores. It differs from *D. carpentariensis* sp. nov. in that it lacks a scapular fold, scales in axilla are not reduced in size and not granular, scales on flanks strongly heterogeneous with scattered scales that are distinctly larger than surrounding scales, and a black gular band or black spots on sides of neck.

Remarks. *Diporiphora jugularis* is restricted to the Cape York Peninsula and has been referred to as *D. bilineata* owing to the lack of a gular fold (e.g. Cogger, 2014; Wilson and Swan, 2017). The distribution maps for *D. bilineata* usually show a distribution (e.g. Cogger, 2014; Wilson and Swan, 2017), with most of the range in the NT extending across the Gulf of Carpentaria region of Queensland and onto the Cape York Peninsula. However, genetic work has shown that the Cape York Peninsula population is not closely related to *D. bilineata* and is instead the sister lineage to *D. australis* (Edwards and Melville, 2010), from which it is distinguished by lacking a gular fold (as opposed to a gular fold being present in *D. australis*).

There are a number of names available for *Diporiphora* on the Cape York Peninsula. Examination of specimens held in the type collection at the NHMUK showed that the earliest known treatment of this species was in 1867 by Günther. As detailed above for *D. australis*, *Grammatophora calotella* is a replacement name created by Günther in 1867 for a species described earlier in the same year by Steindachner. The *Grammatophora calotella* treatment was based on BMNH 66.12.28.22–23, but these specimens are the taxon from Cape York Peninsula (i.e. *D. jugularis*). However, because *Grammatophora calotella* Günther, 1867 is a replacement name for *Calotella australis* Steindachner, 1867 and the

account contains no description of that species, these BMNH specimens have no type status. Thus, the first valid description of this species was in 1877: *Grammatophora jugularis* Macleay.

(b) *D. bennettii* species group (fig. 1)

Content:

D. albilabris Storr, 1974
D. bennettii (Gray, 1845)
D. perplexa sp. nov.
D. sobria Storr, 1974

Diagnostic characters for group (Table 2):

- two canine teeth on each side of upper jaw (fig. 2)
- scales in axillary region not granular
- lateral dark spot in axilla, if present.

Remarks

The *D. bennettii* species group is widely distributed across northern Australia from the Kimberley to north-western Queensland (fig. 8). This species group has moderate size overall, with *D. sobria* and *D. perplexa* sp. nov. attaining maximum sizes of <70 mm SVL, and with the two Kimberley endemics reaching only 61 mm SVL (*D. albilabris*) or 55 mm SVL (*D. bennettii*).

A key character in distinguishing the *D. bennettii* species group from the other species groups in northern Australia, and in particular the broadly sympatric *D. bilineata* species group, is the number of canine teeth on each side of the upper jaw (fig. 2). Agamid lizards have two kinds of teeth: acrodont, which are fused to the jaw and constitute most of the teeth running along the extent of the jaw, and pleurodont, which sit in sockets (Richman and Hadrigan, 2011). The canines in *Diporiphora* are pleurodont teeth. In all members of the *D. bennettii* species group, there are two canines on each side of the upper jaw, where the posterior pleurodont tooth is usually slightly larger than the anterior tooth, a possible consequence of the tooth replacement process. In contrast, all of the species in the *D. bilineata* and *D. australis* species groups have a single canine on each side of the upper jaw. This variation in tooth number is consistent within these species groups. However, in some juvenile and hatchling lizards, the pleurodont teeth may be absent or not fully enlarged, so this character is best used to distinguish adult lizards from each species group.

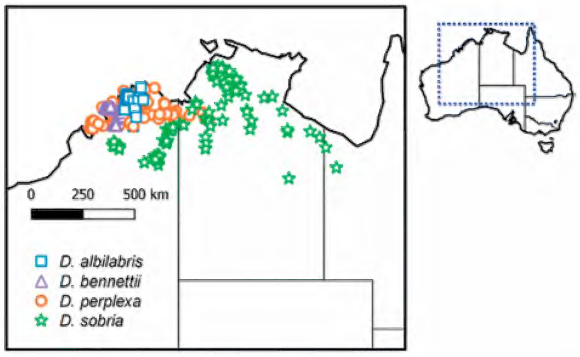

Figure 8. Distributions of *D. albilabris*, *D. bennettii*, *D. sobria* and *D. perplexa* sp. nov. based on specimens examined and collection records.

Owing to the structure of the tree in this group (fig. 2c), major changes to the current taxonomy are required. From the molecular data, we recovered a sister relationship between true *D. bennettii* (i.e. a small-bodied north-west Kimberley form) and *D. albilabris albilabris*. Sister to this pair was a monotypic lineage with specimens assigned to either *D. albilabris sobria* or *D. bennettii arnhemica*, which indicated that the latter two subspecies were a single species. Lastly, an unnamed species that was assigned to *D. bennettii* but lacked the short body and tail of the holotype was sister to these three lineages.

To resolve conflicts with subspecies and stabilise the taxonomy, several changes were necessary. First, *D. albilabris albilabris* was raised to full species because its sister taxon is the distinctive true *D. bennettii*. Next, we raised *D. albilabris sobria* to full species and synonomised *D. bennettii arnhemica* with *D. sobria* owing to page precedence in Storr's (1974) original descriptions (*sobria* – p. 135; *arnhemica* – p. 137). With the description of the widespread taxon usually attributed to *D. bennettii* (i.e. *D. perplexa* sp. nov.), we feel stability has been achieved in this species group from these taxonomic changes. Should further work show structure in the *D. sobria* lineage, then the name *D. arnhemica* would be available if it corresponded to an unnamed lineage. But at this point, there is insufficient evidence from genetic work and morphology to warrant recognition of two taxa within this group.

***Diporiphora albilabris* Storr, 1974**

Common name. White-lipped two-lined dragon.

Figure 9, Tables 3, 4

Diporiphora albilabris albilabris Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [133]. Type data: holotype – WAM R43517, Mitchell Plateau, WA [14° 48' S, 125° 50' E].

Diagnosis. Body size moderate (to 61 mm SVL), tail moderately long (from 1.8–2.5 × SVL). Gular and post-auricular folds present; scapular fold absent. White dorsolateral stripes on raised scale rows. Lacks dark smudge on posterior of tympanum. Scales between dorsolateral stripes are heterogeneous (fig. 10a), with paravertebral row reduced, 2nd paravertebral row enlarged. Pre-cloacal pores 4; femoral pores 2.

Description of holotype. Female. 44 mm SVL, 94 mm tail length. Small body size, moderately robust with long limbs and tail. Two canines on either side of upper jaw. Gular and post-auricular folds present, scapular fold absent. Dorsal scales heterogeneous, with dorsolateral row of enlarged, strongly keeled white scales running from back of head to pelvis and forming well-defined white dorsolateral stripes. Paravertebral rows, either side of the vertebral scale row, are reduced in size compared with adjacent scale rows, leading to the scales of the paravertebral and adjacent scale rows being strongly heterogeneous. To the outer edge of the white dorsolateral stripes, scales are relatively small and keeled,

with keels angling toward ventral surface at midbody. Scales on flanks are heterogeneous with scattered slightly enlarged scales. Scales on limbs and tail not spinose, a row of enlarged pale spines on the post-auricular fold. Scales in axilla not granular. Ventral scales strongly keeled. Pre-cloacal pores 3 (2 right; 1 left); femoral pores 2.

Dorsum pattern complex. Wide (~3 scales) poorly defined grey vertebral stipe and prominent white dorsolateral lines from back of head to base of tail. Five wide dark transverse bands between dorsolateral stripes between head and pelvis. Dark bands extend irregularly from the outer side of the white stripes, fading into the colour patterns on the sides. Dark bands are narrower, approximately half the width, than the pale interspaces with background colour. Head strongly patterned: poorly defined line of pale scales from back of eye, over top of ear towards white dorsolateral stripes, although not contacting stripes; labials pale cream, with a few darker flecks, extending as a broad pale band along jaw to back of head and ending at the enlarged spinose scales on the post-auricular fold. Lacks dark spot on posterior of tympanum. Lateral surfaces distinct from dorsum, with sides dark brown with light brown spots, the spots consisting of clusters of 2–4 pale scales on the dark brown scales. Lateral stripe between axilla and groin absent. Lateral dark spot absent Arms weakly banded with dark bands approximately the same width as intervening pale colour. Banding on legs not well defined, dark bands on anterior two-thirds of tail, with dark bands wider than the light bands, fading to unbanded for remainder of tail. Gular region with six grey longitudinal stripes ending at gular fold, ventral surface of torso and tail with cream colouration and unpatterned.

Figure 9. *Diporiphora albilabris*: a, adult male in breeding colouration (registered specimen NMV D73860) from King Edward River crossing, Western Australia (photo: J. Melville); b, dorsal view of holotype WAM R43517, Mitchell Plateau, Western Australia.

Variation. 43–61 mm SVL; 92–125 mm tail length. Tail long, ranging from 1.8–2.5 × SVL. Usually a spine above tympanum, with several spines along post-auricular fold. A short row of spines extends from post-auricular fold to above tympanum, variably expressed with most reaching less than half way to tympanum. Nuchal crest absent to very low in profile. On dorsum, paravertebral row sometimes approaches the size of vertebral row, but is typically reduced in size. The enlarged dorsolateral row decreases in size posteriorly, reaching normal size at the base of the tail.

Dorsal patterning variable and complex with 5–6 dark brown bands from nape to legs between dorsolateral white stripes, intersected by a poorly defined vertebral stripe of grey, approximately 3 scales wide. These dark bands extend irregularly to the outer side of the white stripes, fading into the colour patterns on the sides, which are dark brown with light brown spots. Dorsal patterning tends to be obscured in males in full breeding colouration, where they have strongly contrasting charcoal black, white and chestnut or orange-red colouring on head and upper body, with ventral surface of head, chest and tail also having an orange-red flush in some individuals. Labial scales pale cream with a few darker flecks, extending as a broad pale band along jaw to back of head ending at the enlarged spinose scales on the post-auricular fold. Ventral surface of head often has grey longitudinal stripes ending at gular fold. Ventral surface of body and tail unpatterned and cream in colour.

Distribution and ecology. Restricted to the central and northern Kimberley region (fig. 8). Most records are from the Mitchell Plateau and Prince Regent River National Park, with other records from Kalumburu, Theda and Doongan stations. No specimens known from islands.

A habitat generalist occurring in tropical savannah woodlands and grasslands. Although it occurs in savannah woodlands, it appears to be found in rockier areas within these habitats, including laterite, basalt and sandstone. Observed to perch on rocks or termite mounds.

Comparison with other species. The distribution overlaps a number of other *Diporiphora* species in the Kimberley. From *D. sobria* it can be distinguished in lacking a scapular fold and having strongly heterogeneous scales between the pale dorsolateral stripes. It differs from *D. perplexa* sp. nov. in having heterogeneous dorsal scales, 2 (vs. 0) femoral pores and no dark markings on the tympanum. It differs from *D. magna* in having a gular fold, femoral pores, double canine teeth in upper jaw and white labial scales. It differs from *D. margaretae* in having a gular fold and double canine teeth on each side of upper jaw.

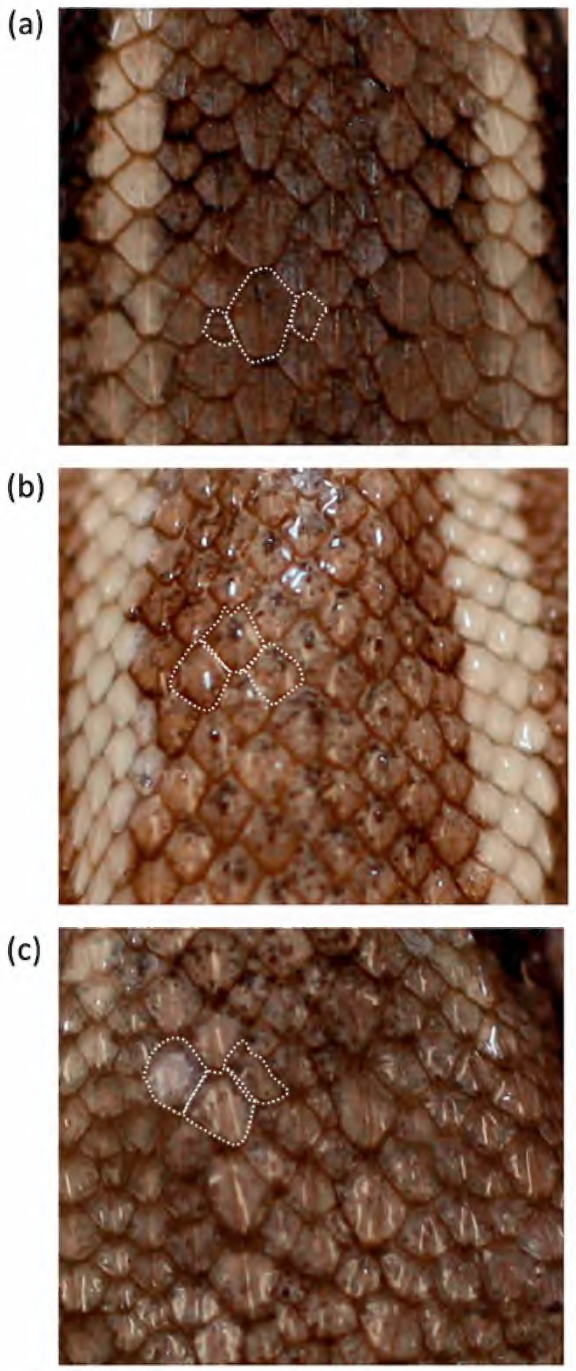

Figure 10. Images of dorsal scales of *D. albilabris* and *D. sobria*, depicting: a, heterogeneous dorsal scales in *D. albilabris*; b, homogeneous dorsal scales in *D. sobria* from Western Australia; c, moderately heterogeneous dorsal scales in *D. sobria* from northern and eastern Northern Territory.

Remarks. Originally a nominate subspecies, elevated here to full species (see account above). Although, based on mtDNA, this species is sister to *D. bennettii*, with which it overlaps in distribution, it is quite different in appearance. *Diporiphora albilabris* has a more typical *Diporiphora* appearance of slender body shape and contrasting markings on the dorsum, whereas *D. bennettii* has a more derived morphology of small body size, short tail length and lack of highly contrasting dorsolateral stripes. *Diporiphora albilabris* has a relatively small distribution in the northern central Kimberley, yet it is reasonably abundant where it occurs and not under immediate threat, making its conservation status likely to be of least concern.

Diporiphora bennettii (Gray, 1845)

Common name. Kimberley sandstone dragon.

Figure 11, Tables 3, 4

Gindalia bennettii Gray, J.E. 1845. *Catalogue of the specimens of lizards in the collection of the British Museum*. British Museum: London. xxviii+289 pp. [247]. Type data: holotype – BMNH 1946.8.12.77, "N.W. Coast of Australia".

Diagnosis. Small body size (to 55 mm SVL) and short tail (<2.0 × SVL), with robust habitus and wide head with short snout. Gular fold present, post-auricular fold strong, scapular fold weak. Dorsals homogeneous, scales in axilla not granular. Lacks

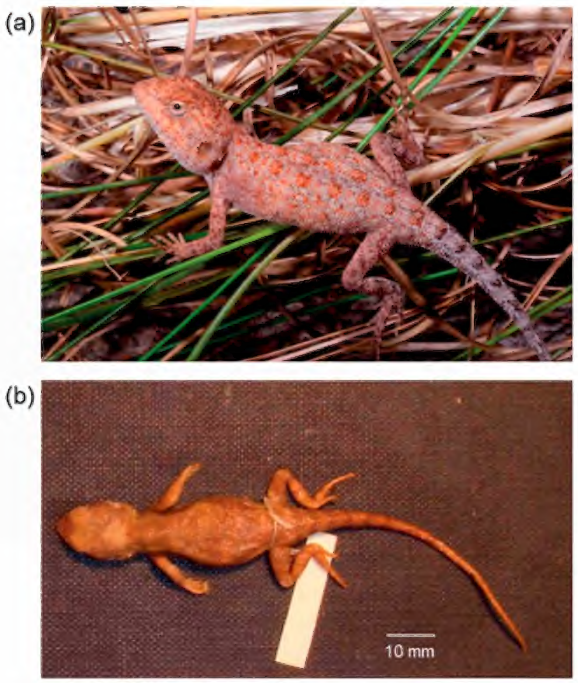

Figure 11. *Diporiphora bennettii*: a, adult from Little Mertens Falls area, Mitchell Plateau, Western Australia. (photo: S. Wilson); b, holotype BMNH 1946.8.12.77, from the "NW coast of Australia", showing dorsal view.

dorsolateral stripes. Usually lacks dark smudge on tympanum, although some individuals have a faint dark spot on posterior edge of tympanum. Pre-cloacal pores 2; femoral pores 0.

Description of holotype. Female; 50 mm SVL; 68 mm tail length. Small body size with wide head and short wide neck. Two canines on either side of upper jaw. Gular fold present. Strong post-auricular fold, weak scapular fold. Post-auricular fold with 1–3 spines. Dorsal scales mostly homogeneous, strongly keeled with keels parallel to midline forming lines running longitudinally down dorsum from shoulders to one third of the way down the tail; enlarged scales associated with vertebral or dorsolateral stripes are absent. Scales on flanks homogeneous, with keels angled towards dorsum. Lacks spinose scales on limbs or tail. Scales in axilla not granular. Weakly keeled scales on ventral gular region and strongly keeled scales on ventral torso. Pre-cloacal pores 2; femoral pores 0.

Dorsum patterning faint and diffuse. Lacks vertebral or dorsolateral stripes. Lacks visible dark transverse bands between head and pelvis. Head virtually unpatterned, without pale labials or pale line between eye and ear. Faint dark spot on posterior of tympanum. Flanks similar to dorsum, with sides of torso being slightly darker than dorsum with a few light brown spots. Lateral stripe between axilla and groin absent. Lateral dark spot absent. Very faint banding on lower hind limbs, dark banding on tail, with light bands much wider than darker bands. Arms lack dark banding. Ventral surface of head, torso and tail unpatterned and cream colouration.

Variation. 41–55 mm SVL, 53–83 mm tail length. Tail short, less than 2.0 × SVL. Gular fold ranges from weak to strong, always with reduced scales along fold, even if skin does not fold over; post-auricular fold strong and scapular weak. Head triangular with usually pronounced adductor muscles, snout short. Typically, one or two enlarged spinose scale above tympanum and on post-auricular fold, with 0–3 adjacent slightly enlarged scales. No conspicuous nuchal crest, but occasionally slightly raised scales present. Dorsal scales homogeneous with no abrupt demarcation of dorsal and lateral scale sizes. Keels of scales on sides angled dorsally and posteriorly. Scales above cloaca on sides of tail at base with raised keels. Tail short, terminating in a blunt tip.

Background colour an admixture of dark brown, tan and pale white scales generating a rather diffuse background pattern with no highly contrasting dorsolateral stripes. Dark brown cross-bands obscure, but in some heavily marked individuals they can form loose networks that enclose pale spots. In some individuals, especially juveniles, there are alternating wide dark brown blotches and thinner pale lines along the dorsum, although these are usually interrupted by variable admixture of different-coloured scales. Lateral surfaces tend to be darker with pale stippling. Tails with thin dark bands with wide pale interspaces. Usually lacks dark spot on tympanum. Ventral surface pale with occasional dark stippling on chin, sometimes extending to ventrum.

Distribution and ecology. Restricted to the northern Kimberley (fig. 8), with many records from the Mitchell Plateau and Prince Regent River National Park, extending east to Drysdale River National Park and including a few neighbouring offshore islands: Augustus, Darcy and Unwins.

Collection records (over 40) are nearly all from sandstone rock outcrops and escarpments with spinifex cover.

Comparison to other species. This species is similar to *D. perplexa* sp. nov., with extensive distributional overlap and occurring in similar habitats, but differs in having a much smaller body size, a short tail and no dorsolateral stripes. It differs from *D. albilabris* in having a smaller body size, a short tail, no femoral pores, homogeneous dorsal scales and in pattern by lacking any prominent vertebral or dorsolateral stripes. It differs from *D. magna* and *D. margaretae* in having a smaller body size, a short tail, a gular fold and a pair of enlarged canines on each side of upper jaw. It differs from *D. pallida* sp. nov. in having two canine teeth on each side of upper jaw.

Remarks. The species was previously believed to include what we describe below as *D. perplexa* sp. nov. *Diporiphora bennettii*, however, is the sister species to *D. albilabris* (fig. 1b; also restricted to the northern Kimberley), with these two being sister species to *D. sobria*, which is now understood to be widely distributed in the southern AMT. *D. perplexa* sp. nov. occurs over a broad area in the Kimberley and extends to the NT, and accordingly, *D. bennettii* is now known to be restricted to the north-west Kimberley. *Diporiphora bennettii* has an unusual morphology for a *Diporiphora*, owing to its small body size, short tail, robust habitus, obscure dorsal patterning and close association with sandstone outcrops in the northern Kimberley. The redefinition of this species and reduction of its range adds to the large number of endemic reptiles and frogs from this region (e.g. Powney et al., 2010; Palmer et al., 2013).

Diporiphora perplexa sp. nov.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:4A6A3A8B-5FB1-40D5-843B-258D095238F3

Common name. Kimberley rock dragon.

Figure 12, Tables 3, 4

Holotype. WAM R177290 (formerly NMV D73819) (adult male), Gibb River Rodd, 20 km west of Ellenbrae Station, WA (15° 57.31' S, 126° 52.9' E). Collected by J. Melville on 9 September 2005.

Paratypes. NMV D73805 (adult female), Home Valley Station, WA (15° 44.39' S, 127° 49.83' E); NMV D73841 (adult female), King Edward River Campground, Mitchell Plateau Road, WA (14° 56' 57.1" S, 126° 12' 10.4" E); NMV D73978 (adult male), Buchanan Highway, south of Jasper Creek, NT (16° 02' 46.8" S, 130° 51' 49.3" E); NMV D73980 (adult female), Bullo Road off Victoria Highway, NT (15° 48' 39.2" S, 129° 40' 13.5" E); WAM 119719 (male), Emma Gorge, Cockburn Range, WA (15° 50' S, 128° 02' E); WAM R162517 (female), 25 km S Wyndham, WA (15.7154° S, 128.2684° E); WAM R171418 (male), Prince Regent River National Park, WA; WAM R175785 (female), Waterfall Yard, 15 km N Mt Elizabeth Homestead, WA (16.2822° S, 126.1059° E).

Diagnosis. Body size moderately large (to 68 mm SVL) with long tail (1.9–2.5 × SVL). Gular and scapular folds present but weak; post-auricular fold strong. Homogeneous dorsal scales. Pale dorsolateral stripes from back of head to one-third down torso. Black smudge on posterior edge of tympanum, extending on to scales posterior to tympanum. Pre-cloacal pores 2–4; femoral pores 0.

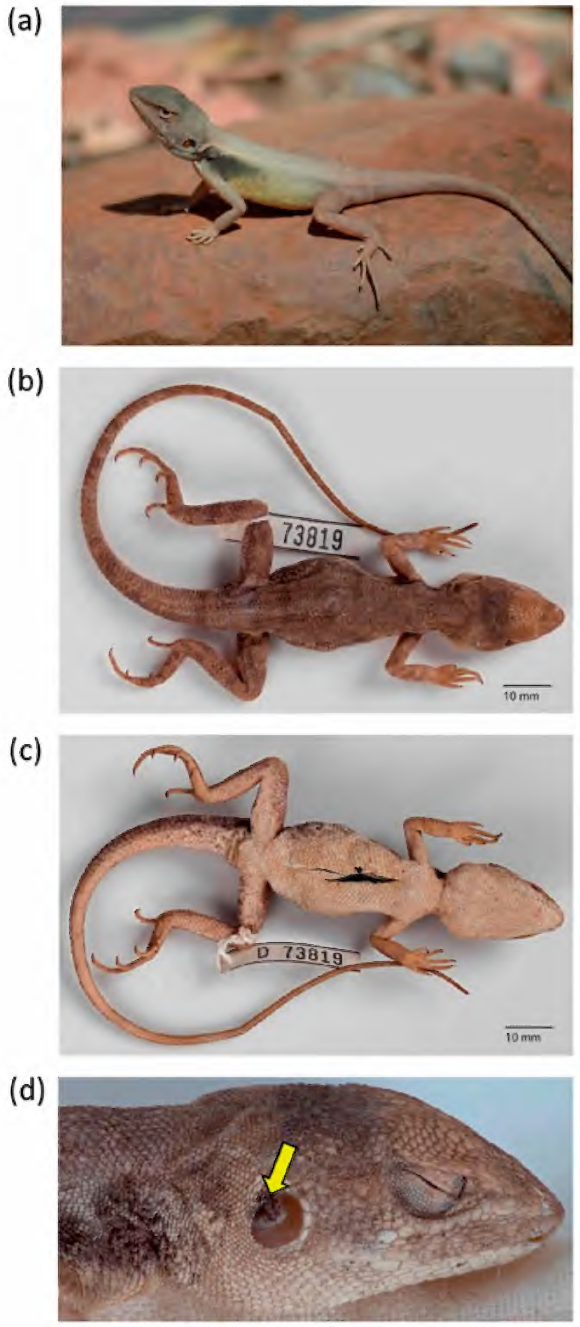

Figure 12. Holotype of *Diporiphora perplexa* sp. nov. (WAM R177290, formerly NMV D73819): a, in life – adult male in breeding colouration from Gibb River Road, west of Ellenbrae Station, Western Australia; b, c, d, preserved specimen in dorsal, ventral and lateral (head) views. Yellow arrow highlights a key diagnostic character: dark pigment "smear" on posterior of tympanum spreading onto neighbouring head scales (photos: J. Melville).

Description of holotype. Male; 63 mm SVL; 140 mm tail length. Moderately stout with long tail and limbs. Two canines on either side of upper jaw, with posterior canines extremely enlarged relative to anterior canines. Gular fold present but weak. Strong post-auricular fold, weak scapular fold. Dorsal scales homogeneous, strongly keeled with keels parallel to midline forming lines running longitudinally down dorsum from shoulders to base of the tail; enlarged scales associated with vertebral or dorsolateral stripes not conspicuous. Scales on flanks homogeneous, with keels on posterior flanks angled towards dorsum. Lacks spinose scales on head, limbs and tail. Scales in axilla small but not granular. Ventral scales weakly keeled in gular region and strongly keeled on body. Pre-cloacal pores 2; femoral pores 0.

Dorsum patterning faint. Lacks vertebral stripe and faint dorsolateral stripes from back of head to one-third down torso. Lacks visible dark transverse bands between head and pelvis. Head relatively unpatterned: labials same colour as rest of head; and faint, narrow pale line from posterior of eye to above ear. Prominent black smudge on posterior edge of tympanum, extending onto scales behind ear. Flanks have large dark patches in axillary region extending up onto shoulder, then extending posteriorly and fading to dark speckled appearance on a pale background. Lateral stripe between axilla and groin absent. Large lateral dark patch in axilla, extending up onto shoulder. Arms lack dark banding. Very faint banding on hind limbs and tail, with light bands much wider than darker bands. Ventral surface plain cream to white.

Variation. 48–76 mm SVL; 101–183 mm tail length. Tail long, ranging from 1.9–2.5 × SVL. In some individuals keeling on dorsal scales converge towards the midline approximately halfway down torso but run parallel to midline from mid-dorsum to pelvis. Usually a single spinose scale above tympanum, with 1–3 spines on post-auricular fold, occasionally with a short row of spines extending from post-auricular fold to above tympanum. Dorsolateral scale rows raised on neck. In some individuals, a slightly raised nuchal crest (males) and the scales of dorsolateral rows on body appear to be enlarged with slightly thickened keels, but this is barely perceptible (hence, we have not included it as a diagnostic character). Pre-cloacal pores were usually 2, but many had 4; no specimens with femoral pores.

Dorsal colouration variable from strongly patterned (mainly smaller individuals and females) to unpatterned (adult males). Most individuals have pale dorsolateral stripes running from the back of the head to at least a third of the way down the torso. In strongly patterned individuals, these stripes continue onto the tail where they converge approximately halfway down. More patterned individuals have 5–7 dark cross-bands between the pale dorsolateral stripes, continuing onto the tail. These cross-bands are intersected by a narrow pale white, cream or grey vertebral stripe. Also, these individuals will often have a black patch on shoulder, into the axilla, with pale flecks. Individuals with little patterning are usually adult males with breeding colours, which includes a large black patch in axillary region extending up onto shoulder, then posteriorly fading to dark speckled appearance with a bright yellow background,

and a pink flush on tail and rear legs. No distinct patterning on head, upper labials flecked with light brown and cream, with no pale labial stripe. Ventral surfaces plain cream to white. Gular region plain or with diffuse brown speckling (no lines).

Distribution and ecology. Widespread in the Kimberley and extreme western Top End of the NT. They occur from the Yampi Peninsula in the south-western Kimberley, extending eastwards to the Kununurra area and to the western NT in the Jasper Gorge area.

This species is almost always associated with rocks. It will also climb onto vegetation, such as cane grass, small shrubs and trees, spinifex and even pandanus and mangroves, but with rocks or creek lines nearby.

Etymology. Named from the Latin for confused or cryptic, in reference to Allan Greer's (former curator at the AMS) thoughts on this species when carrying out earlier work on the group in the 1990s. This species remained hidden until a genetic analysis and consultation of the *D. bennettii* type with its small body size, short tail and diffuse pale patterning.

Comparison with other species. Similar to *D. bennettii*, occurring in similar rocky habitats, but differs in having a long tail and limbs and dorsolateral stripes. Can be distinguished from *D. albilabris* and *D. sobria* in mostly lacking femoral pores, having no white or pale stripes on the head (on upper labials or between eye and ear), no stripes under chin and homogenous dorsal scales. Differs from *D. magna, D. margaretae* and *D. pindan* in having a gular fold, a black spot on tympanum and two canine teeth on each side of upper jaw. *Diporiphora lalliae* differs from *D. perplexa* sp. nov. in lacking both a black spot on tympanum and double canine teeth on each side of upper jaw.

Remarks. This species has previously been confused with *D. bennettii* (see account above), and this is the species usually depicted in field guides as *D. bennettii*. However, both genetic work and examination of the original specimens have now distinguished these two species. Interestingly, *D. perplexa* sp. nov. is the only member of the *D. bennettii* species group that is sympatric with the three other species (which are generally allopatric). This distributional pattern suggests that *D. perplexa* sp. nov. may have different habitat preferences and ecology to the other species that allows for sympatry.

Recent unpublished phylogenomic research using single-nucleotide polymorphisms shows that *D. perplexa* sp. nov. is highly divergent and genetically distinguishable from the *D. sobria* (as defined below), even in areas of syntopy (J. Fenker, unpublished data).

Diporiphora sobria Storr, 1974

Common name. Northern savannah two-pored dragon.

Figure 13, Tables 3, 4

Diporiphora albilabris sobria Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [135]. Type data: holotype – WAM R23180, Pine Creek, NT [14° 04' S, 131° 58' E].

Diporiphora bennettii arnhemica Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. Records of the Western Australian Museum 3: 121–146 [137]. Type data – holotype ANWC R740, near upper Katherine River, NT [14° 13' S, 132° 36' E]. Synonymy decision of current work.

Diagnosis. Body size moderately large (to 69 mm SVL) with moderately long tail (2.3–2.6 × SVL). Gular fold present, post-auricular fold strong and scapular fold present but often weak. Dorsolateral stripes present. Lacks dark smudge on posterior edge of tympanum. In WA, the scales between dorsolateral stripes are homogeneous (fig. 10b); in the NT, heterogeneous (fig. 10c). Pre-cloacal pores 4; femoral pores 2.

Description of holotype. Subadult, unknown sex; 34 mm SVL; 68 mm tail length. Moderately robust with long limbs and tail. Two canines on either side of upper jaw. Gular fold present, scapular and post-auricular folds present but weak. Dorsal scales homogeneous between faint pale dorsolateral stripes. These homogeneous scales are relatively large and strongly keeled. On the outer sides of the faint dorsolateral stripes are smaller keeled scales. Scales on flanks homogeneous, with keels running parallel to dorsum. Lacks spinose scales on head, limbs or tail. Lacks granular scales in axilla. Ventral scales homogenous and strongly keeled. Pre-cloacal pores 4; femoral pores 2.

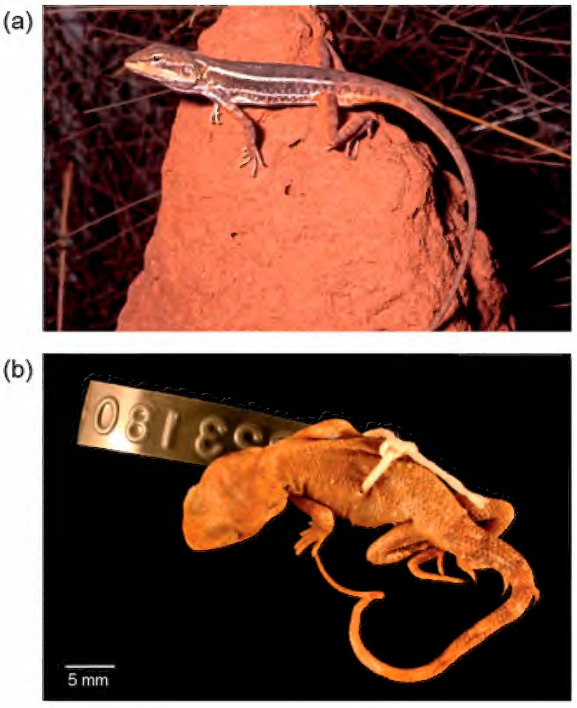

Figure 13. *Diporiphora sobria*: a, adult male with breeding colouration, Halls Creek, Western Australia (photo: S. Wilson); b, holotype WAM R23180 from Pine Creek, Northern Terrotory.

Dorsal colour uniform brown and grey tones, without apparent patterning. Lacks vertebral stripe but has faint dorsolateral stripes on anterior half of body, fading to background colour midway down torso. Lacks visible dark transverse bands between head and pelvis. Head relatively unpatterned: labials pale; and very faint, narrow pale line from posterior of eye to above ear. Dark smudge on posterior of tympanum absent. Flanks unpatterned and consistent with dorsal colouration. Lateral stripe between axilla and groin absent. Lacks lateral dark patch. Arms lack dark banding. Very faint banding on hind limbs; dark bands on anterior two-thirds of tail, with dark bands being narrower than the light, fading to unbanded for remainder of tail. Ventral surface of head, torso and tail unpatterned and white or cream colouration.

Variation. 46–69 mm SVL; 114–162 mm tail length. Tail long, ranging from 2.3–2.6 × SVL. Gular fold always present and often strong, post-auricular fold from weak to strong and scapular fold present but variable. No low nuchal crest. Most individuals have homogeneous dorsal scales between pale dorsolateral stripes, with all individuals examined from WA having homogeneous scales. However, animals examined from the eastern NT, on the Barkly Tablelands and the Gulf of Carpentaria region, and from north-central regions, such as the Mt Wells and Pine Creek area, had somewhat heterogeneous scales between pale dorsolateral stripes. In these animals, paravertebral rows on either side of the vertebral scale row are not reduced in size in comparison to the vertebral scale row, but the 2nd paravertebral scale row is slightly enlarged, with a strong central keel that is aligned to the scales immediately anterior and posterior. These strongly keeled scales that are aligned form a ridge running along the dorsum either side of the midline. Animals with these dorsal scales include NMV D72666–68, D72706, D72707, D72715, D72720, D73995, D74001, D74003, D74022, D74024 and D74262. Scales on the sides are similar to typically sized dorsal scales and are angled up towards midline. Ventral scales homogenous and strongly keeled. Pre-cloacal pores 4 (occasionally up to 5); femoral pores 2 (occasionally 3 or 4).

Dorsal patterning variable from plain to strongly patterned. Strongly patterned individuals, typically adult females and juveniles, have approximately 7–9 irregular dark transverse bands from nape to legs across dorsum on a pale background. Dark bands are of similar width or narrower than pale background. These bands are separated by an indistinct faint grey or light brown vertebral stripe. The dark transverse bands continue laterally beyond the pale cream dorsolateral stripes, becoming diffuse and terminating on sides, with defined lateral stripe absent. Labial scales pale cream, with a few darker flecks, extending as a broad pale band along jaw to back of head ending at the post-auricular fold. In these animals, the lateral surfaces of the neck, axilla and flanks lack a defined dark patch. Some individuals are less strongly patterned, particularly in the NT, and lack the pale dorsolateral stripes or the dorsolateral stripes fade midway down dorsum. Adult males in breeding colouration often have little patterning, having strongly contrasting charcoal black, white and chestnut or orange-red colouring on head, flanks and upper body, with tail also having a pink flush in some individuals. Arms and legs banded. Ventral surface of head, torso and tail usually unpatterned and white or cream colouration. However, adult males may have up to three pairs of grey stripes in gular region, terminating at gular fold.

Distribution and ecology. Widely distributed from the southern Kimberley region (i.e. south of the barrier ranges: King Leopold and Durack), Top End of the NT (but with no records from Arnhem Land) and just extending into western Queensland (fig. 8). Extends south to the Katherine area.

A habitat generalist occurring in tropical savannah woodlands and grasslands, within these habitats it appears to be associated with rockier areas. Similar habitats to *D. albilabris*. Seen to perch on low vegetation, rocks or termite mounds.

Comparison with other species. This species has a very wide distribution and overlaps with numerous other *Diporiphora* species. In WA, it can be distinguished from *D. albilabris* in having a scapular fold, fewer spines around tympanum and post-auricular fold and having homogenous scales between the dorsolateral stripes. It differs from *D. perplexa* sp. nov. in having pale rows of dorsolateral scales, usually a strong post-auricular fold, two femoral pores and lacks dark markings on the posterior of the tympanum. Differs from *D. bilineata, D. magna* and *D. lalliae* in having femoral pores, two pairs of canines in upper jaw and white labial scales. It also differs from *D. bilineata*, *D. magna* and *D. margaretae* in having a gular fold and two pairs of canine teeth on each side of upper jaw.

Remarks. This species incorporates what was *D. arnhemica* and much of the distribution of *D. albilabris albilabris sensu lato*. Despite the original name, this species does not appear to occur in Arnhem Land from our observations, although collections from this region are scarce. This taxon is diverse and exhibits morphological variation in dorsal scalation. Where it occurs near the morphologically similar *D. albilabris* in the Kimberley region, the homogeneous dorsal scalation differs and separates the two species.

(c) *D. bilineata* species group (fig. 1c)

Content:

D. bilineata Gray, 1842
D. lalliae Storr, 1974
D. magna Storr, 1974
D. margaretae Storr, 1974
D. gracilis sp. nov.
D. granulifera sp. nov.
D. carpentariensis sp. nov.

Diagnostic characters for group (Table 2):

- one canine tooth on each side of upper jaw
- granular scales in axilla present, with the exception of *D. lalliae*
- lateral dark spot in axilla
- femoral pores absent.

Remarks

The *D. bilineata* species group is widely distributed across northern Australia (fig. 14), from the Kimberley to the Cape York

Peninsula. Almost all species appear to be generalists, with the possible exception of *D. gracilis* sp. nov. being specialised for grasses. Body size ranges from small (*D. margaretae*, to 55 mm SVL) to large (*D. magna*, to 77 mm SVL). This is a genetically diverse species group (Smith et al., 2011) for which there has been significant difficulty in species delimitation based on morphology. We provide species accounts for *D. bilineata*, *D. lalliae* and *D. magna,* with key morphological characters for species identification and a revision of their distributions. We also raise *D. margaretae* from synonymy of *D. bilineata* (Cogger et al., 1983), based on genetic results and examination of types. We also describe three new species: two from Queensland and one from the southern Kimberley.

Diporiphora bilineata Gray, 1842

Common name. Two-lined dragon.

Figure 15, Tables 3, 4

Diporiphora bilineata Gray, J.E. 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany.* Treuttel, Würz & Co: London. [54]. Type data: syntype(s) – BMNH 1946.8.12.75–76, Port Essington, NT.

Diagnosis. Body size moderate (to 58 mm SVL) with long tail (2.2–2.7 × SVL). Gular and post-auricular folds absent, scapular fold present but weak. Granular scales in axilla, extending over arm to neck. Dorsal scales moderately heterogeneous: scales on 2nd paravertebral row and the two rows of pale dorsolateral scales slightly enlarged and raised. Flanks dark in colour with dark colour of granular scales extending posteriorly onto flanks, which have a speckled appearance due to scattered white scales on the dark background. Pre-cloacal pores 2; femoral pores 0.

Description of syntypes. Males; 57 and 58 mm SVL, 151 and 56 (broken) mm tail length. Medium-sized *Diporiphora*, moderately gracile with long limbs and long tail. One canine on either side of upper jaw. Gular and post-auricular folds absent, scapular fold present. Dorsal scales heterogeneous; vertebral row of scales, plus the 3–4 rows immediately adjacent on either side, are enlarged and strongly keeled. The vertebral row and the fourth longitudinal scale row from the vertebral are raised. Beyond these enlarged vertebral scales are four rows of small homogenous scales and then a dorsolateral longitudinal row of enlarged scales, with scales on each side strongly keeled. Raised vertebral and dorsolateral scale rows extend up onto neck onto the back of head and posteriorly onto tail. Scales on flanks homogeneous, although changing from small granular scales in

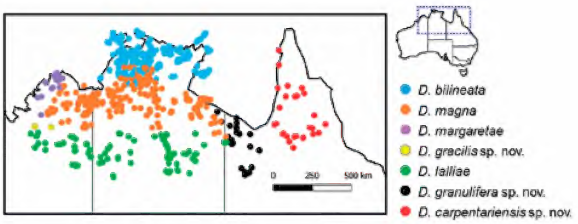

Figure 14. Distributions of *D. magna*, *D. bilineata*, *D. lalliae*, *D. margaretae*, *D. gracilis* sp. nov., *D. granulifera* sp. nov. and *D. carpentariensis* sp. nov. based on specimens examined and collection records.

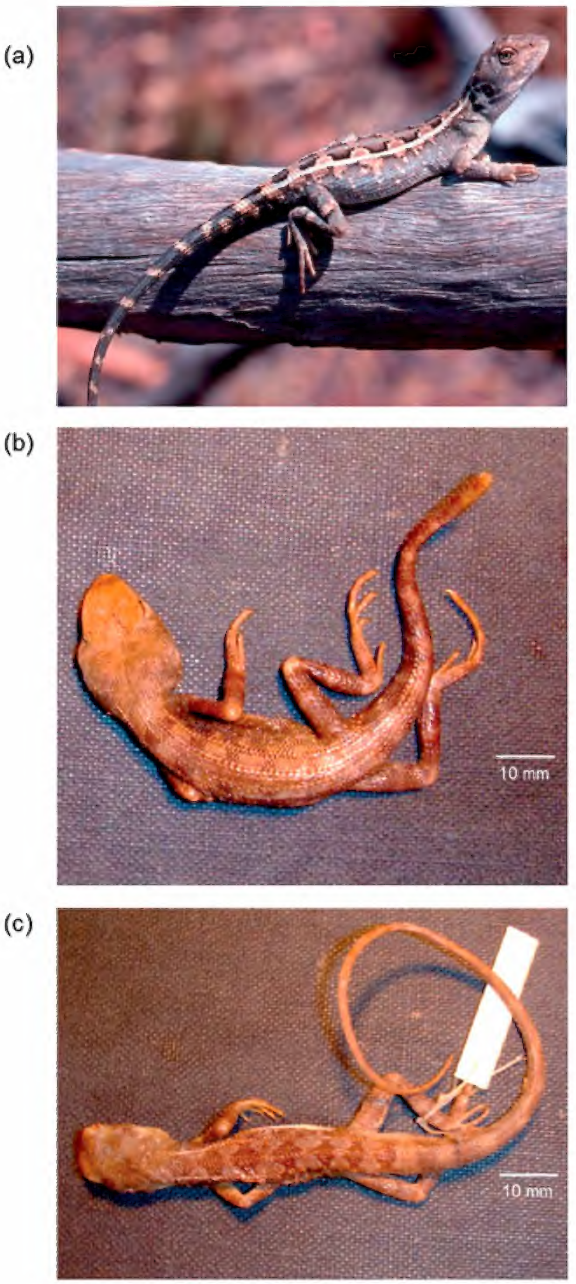

Figure 15. *Diporiphora bilineata*: a, adult in non-breeding colours, Casuarina, Northern Territory (photo: S. Wilson); b, syntypes BMNH 1946.8.12.75–76, Port Essington, Northern Territory.

axilla to small but non-granular scales on the posterior two-thirds of flanks. A few small pale spinose scales at back of head on each side, lacks spinose scales on limbs or tail. Granular scales in axilla, extending over arm onto neck. Ventral scales strongly keeled. Pre-cloacal pores 2; femoral pores 0.

Dorsum strongly patterned. Wide pale, poorly defined vertebral stripe associated with enlarged vertebral scale rows and narrow pale dorsolateral stripes associated with row of enlarged scales, extending from back of head onto base of tail. Six dark transverse bands between head and pelvis, narrower than the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Flanks dark in colour with dark colour of granular scales extending posteriorly onto flanks, which have a speckled appearance due scattered white scales on the dark background. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up onto shoulder. Arms and legs lack dark banding. Faint banding on hind limbs; dark bands down length of tail, with dark bands being wider than the light bands. Ventral surface cream with no patterning.

Variation. 46–58 mm SVL; 113–156 mm tail length. Tail long, ranging from 2.2–2.7 × SVL. Gular fold always absent and scapular fold present in all animals examined. In a few specimens a small post-auricular fold present. Outer raised trailing edge of scales on outer row of dorsolateral stripes usually present but often trailing edge of scales are only weakly raised, providing demarcation between dorsal and lateral surface. Pre-cloacal pores 2; femoral pores 0.

Variable patterning from strongly patterned to plain individuals. In patterned individuals, 5–7 dark brown transverse bands ranging from narrower to wider than pale background. Dark bands are offset to each other on either side of a narrow greyish or cream vertebral stripe and intersected two pale dorsolateral stripes. In plain individuals, dark dorsal transverse bands are faint or absent, vertebral stripe may be absent but there are usually still the pale dorsolateral stripes from neck to at least level of mid-dorsum. However, dorsolateral stripes are also absent in a few animals. Granular scales on flanks around arm are usually dark brown, extending posteriorly onto flanks that have speckled appearance due to scattered white scales on a dark background. These scattered pale scales sometimes form vertical lines. No white markings on face, labial scales speckled with light brown flecks. Usually faint or no banding on legs but in some more patterned animals banding present. Ventral surface cream, usually plain but some individuals have faint longitudinal stripes on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a yellow wash over the head and upper body with a large black patch in axilla that extends onto shoulder.

Distribution and ecology. *Diporiphora bilineata* is widely distributed across the Top End of NT. It occurs sympatrically with *D. magna* in the Pine Creek area. It is a common generalist that occurs throughout the tropical savannah woodlands and grasslands of this region, and is often seen perching on low vegetation, rocks or termite mounds.

Comparison with other species. The distribution of *D. bilineata* overlaps with two other *Diporiphora* species. *Diporiphora bilineata* can be distinguished from *D. magna* in usually having fewer pre-cloacal pores (2 vs. 4), lacking a post-auricular fold and by possessing heterogeneous dorsal scales, rows of enlarged vertebral scales and dark flanks with scattered white scales. *Diporiphora bilineata* can be distinguished from *D. sobria* in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw.

Remarks. This taxonomic revision has reduced the distribution of this species to the Top End of the NT, with overlap with *D. magna* in the Pine Creek area. Previously, adult males of *D. bilineata* in breeding colouration may have been mistaken for *D. magna*, and *D. jugularis* has been resurrected that was often attributed to *D. bilineata*, further reducing this species' range. Genetic work has shown that these two species do not overlap extensively (Smith et al., 2011).

Diporiphora lalliae Storr, 1974

Common name. Northern deserts dragon.

Figure 16, Tables 3, 4

Diporiphora lalliae Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [138]. Type data: holotype – WAM R23020, Langey Crossing, WA [17° 39' S, 123° 34' E].

Diagnosis. Body size moderately large (to 62 mm SVL) with very long tail (2.6–3.4 × SVL). Gular, post-auricular and scapular folds present. Small scales in axilla but usually not granular. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

Description of holotype. Male; 62 mm SVL; 152 mm tail length. Medium-large *Diporiphora* with long tail and long limbs. One canine on either side of upper jaw. Gular fold present. Strong scapular and post-auricular folds. Dorsal scales homogeneous, relatively large and strongly keeled. At the shoulder, dorsal scales are raised and strongly keeled (but not enlarged) in a longitudinal series of paravertebral and dorsolateral scales that fade by midbody. Scales on flanks homogeneous. Single white spinose scale at back of head sitting on ventral end of post-auricular fold, lacks spinose scales limbs or tail. Small scales in axilla but not granular. Ventral scales strongly keeled. Pre-cloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Wide grey vertebral stripe (~4 scales wide at middle of dorsum), extending from back of head onto base of tail. Prominent pale dorsolateral stripes from shoulder to mid-dorsum, fading into background patterning; these scales form the enlarged longitudinal row of dorsolateral scales at the shoulder. Six dark transverse bands between head and pelvis, approximately the same width as the pale background. Head relatively plain with little patterning, labials similar colour to rest of head but have faint pale line between eye and ear. Dark smudge on posterior of tympanum absent.

Flanks pale in colour, similar to dorsum. Lateral stripe between axilla and groin absent. Dark patch in axilla absent. Arms with faint dark banding. Strong well-defined alternating light and dark bands on legs; dark bands on tail, continuing to near end of tail, with dark bands being a similar width to the light bands. Ventral surface white and unpatterned.

Variation. 49–62 mm SVL; 130–194 mm tail length. Very long tail, ranging from 2.7–3.4 × SVL. Gular fold always present, although weak in some individuals. Scapular fold strong and post-auricular fold usually strong, although weak in some individuals. No enlarged spinose scales above tympanum or along post-auricular fold, although the latter may have several slightly enlarged scales. Very low nuchal crest. Outer raised trailing edge of scales on outer row of dorsolateral stripes usually absent, but in some individuals, the trailing edge of scales are weakly raised, particularly over shoulder, providing weak demarcation between dorsal and lateral surface. Pre-cloacal pores 4; femoral pores 0.

Dorsal patterning variable from strongly patterned to little patterning. In strongly patterned individuals, there are 6–8 wide, dark brown transverse bars between shoulders and pelvis, intersected by a wide grey vertebral stripe; pale dorsolateral stripes from neck and usually extending onto tail. At the shoulder, these dorsolateral stripes consist of an enlarged longitudinal row of scales. Usually no patterning on the head, but in some individuals a white stripe between the eye and ear. In more plain individuals, dark transverse bars faint or absent, and vertebral stripe often absent. Pale dorsolateral stripes from neck to tail usually present, even in unpatterned animals. Dark bands on tail, continuing to near tip. Usually well-defined alternating light and dark bands on upper and lower legs. Dark spot in axillary region absent and flanks usually pale, but some individuals have dark lateral spot above and slightly posterior to shoulder. Ventrum plain.

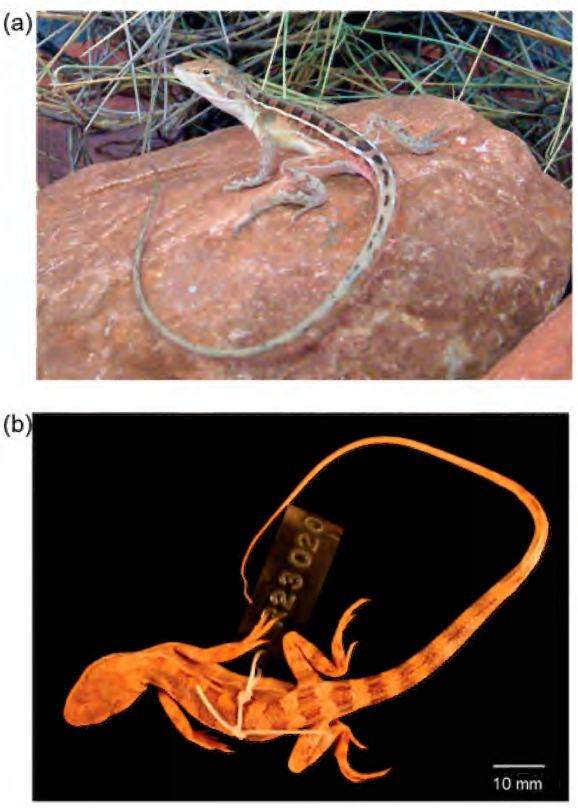

Figure 16. *Diporiphora lalliae*: a, adult male, Three Ways, Northern Territory (photo: S. Wilson); b, holotype – WAM R23020, Langley Crossing, Western Australia.

Distribution and ecology. The distribution of *D. lalliae* spans the northern extent of the arid zone along the western deserts, from the southern Kimberley in WA to the far west of Queensland. It extends into the southern reaches of the AMT but does not occur in the central arid zone as occasionally depicted (e.g. Cogger, 2014).

This species occurs in a variety of habitats from savannah woodlands and grasslands to arid habitats. It is a generalist species that is found in many habitats, often seen perching on small rocks, termite mounds or clumps of earth.

Comparison to other species. *Diporiphora lalliae* is sympatric with *D. magna, D. gracilis* sp. nov. and *D. granulifera* sp. nov. in the northern parts of its range, occurring in similar habitats and is superficially similar in appearance. However, *D. lalliae* can be distinguished from these species by the presence of a gular fold, which is unique in the *D. bilineata* species group (Table 2). The distribution of *D. lalliae* also overlaps with *D. sobria*, from which it can be distinguished in having single canine teeth on each side of upper jaw and lacking femoral pores. In the southern Kimberley region, *D. lalliae* can be distinguished from *D. pindan* in having a gular fold and strong post-auricular and scapular folds.

Remarks. This species has previously been confused with numerous other species owing to its generalised appearance. Phylogenetic work has confirmed that it is a member of the *D. bilineata* species group (Smith et al., 2011) but is unique in this group due to the presence of a gular fold.

Diporiphora magna Storr, 1974

Common name. Yellow-sided two-lined dragon.

Figure 17, Tables 3, 4

Diporiphora magna Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [137]. Type data: holotype – WAM R42786, Old Lissadell (now submerged by Lake Argyle), WA [16° 30' S, 128° 41' E].

Diagnosis. Body size moderately large (to 77 mm SVL) with very long tail (to 3 × SVL). Gular fold absent, post-auricular and scapular folds strong. Granular scales in axilla, extending over arm but not extending onto sides of neck. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

Description of holotype. Female; 47 mm SVL; 141 mm tail length. Medium *Diporiphora*, moderately gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent. Post-auricular and scapular folds strong. Dorsal scales strongly keeled, relatively small and homogeneous. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Cluster of spinose scales at back of head on each side, lacks spinose scales on limbs and tail. Granular scales in axilla, extending over arm but not extending onto sides of neck. Ventral scales strongly keeled. Pre-cloacal pores 3 (2 on right; 1 on left); femoral pores 0.

Dorsum strongly patterned. Wide grey vertebral stripe (~2 scales wide at mid-dorsum), extending from back of head onto base of tail, and prominent pale dorsolateral stripes from shoulder to base of tail, fading into background patterning. Seven dark transverse bands between head and pelvis, narrower than the pale background and offset across the vertebral stripe. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown and strongly defined with an abrupt transition to pale flanks with little patterning. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up onto shoulder. Faint banding on hind limbs; dark bands on anterior two-thirds of tail that are wider than the light bands, fading to unbanded light colouration for remainder of tail. Arms and legs with faint dark banding. Ventral surface cream with a few very faint longitudinal stripes on ventral surface of head.

Figure 17. *Diporiphora magna*: a, adult male, Larrimah, Northern Territory (photo: S. Wilson); b, holotype WAM R42786, Old Lissadell (now submerged by Lake Argyle), Western Australia.

Variation. 54–77 mm SVL; 145–209 mm tail length. Very long tail, ranging from 2.6–3.0 × SVL. Gular fold always absent, post-auricular and scapular strong. In a few individuals, the post-auricular fold, although strong, may be short (<2 mm). Low nuchal crest, more prominent in males. One spinose scale above tympanum and one on post-auricular fold with from 0–3 additional spines on post-auricular fold. Scales rows of dorsolateral stripes on neck and above arms with raised posterior edges. All individuals examined have pre-cloacal pores 4 and femoral pores 0, except for one individual: large male (NMV D73812) from the southern Kimberley has a small indistinct femoral pore on each side.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, 5–7 dark brown transverse bands ranging from narrower to wider than pale interspaces of background colour. Dark bands are often offset to each other on either side of a broad greyish or cream vertebral stripe 3–4 scales wide and two pale dorsolateral stripes usually present. In more plain individuals, dark dorsal transverse bands are faint or absent, vertebral stripe may be absent but with pale dorsolateral stripes from neck to at least level of mid-dorsum. However, dorsolateral stripes are also absent in a few individuals, particularly breeding males. Granular scales in or near the axilla are dark brown, flanks cream, grey, light brown with little patterning. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on legs. Ventral surface cream, usually plain but some individuals have faint longitudinal stripes in gular region. Males with breeding colouration tend to lose some of their dorsal patterning, having a yellow wash over the head and upper body with a large back patch in axilla that extends onto shoulder.

Distribution and ecology. *Diporiphora magna* is widely distributed across the tropical savannah region of northern Australia, from the central Kimberley, WA, through the NT and just over the Queensland border at Lawn Hill National Park. It appears to have been replaced by other *D. bilineata* species group members as follows: to the south by *D. lalliae*, which occupies the northern deserts, to the west in the Kimberley by *D. margaretae* and *D. gracilis* sp. nov., and in the Top End of the NT by *D. bilineata*, although there is a wide (~100 km) area of sympatry between roughly Pine Creek and Katherine.

A habitat generalist occurring in tropical savannah woodlands and grasslands, individuals have been observed to perch on low vegetation, rocks or termite mounds.

Comparison to other species. The distribution of *D. magna* overlaps with numerous other *Diporiphora* species across the tropical savannahs of northern Australia. In the Kimberley region, *D. magna* differs from *D. margaretae* in having a smaller body size (to 77 vs. 55 mm SVL), stronger post-auricular and scapular folds, a longer tail and flanks lacking speckled appearance (scattered white scales on a dark background). In the northern NT, *D. magna* differs from *D. bilineata* in having a post-auricular fold and homogenoous dorsal scales, lacking rows of enlarged vertebral scales and lacking dark flanks with scattered white scales. In the southern part of its range, *D. magna* can be distinguished from *D. lalliae* in lacking a gular fold, a longer tail in proportion to body and granular scales in axilla. Across its range, *D. magna* can be distinguished from *D. albilabris*, *D. bennettii, D. sobria* and *D. perplexa* sp. nov. in lacking a gular fold, lacking femoral pores and having single canines on either side of the upper jaw.

Remarks. Phylogenetic work has redefined the distribution of this species (Smith et al., 2011). Specimens of *D. margaretae* were formerly assigned to *D. magna*, meaning now that *D. magna* does not occur in the north-west Kimberley region. This taxon is diverse and exhibits morphological variation in colour patterning and overlaps or contacts a number of phylogenetically close species. Where it occurs in close proximity to these species, it can be distinguished on the basis of scalation.

Diporiphora margaretae Storr, 1974

Common name. Northwest Kimberley two-lined Dragon.

Figure 18, Tables 3, 4

Diporiphora bilineata margaretae Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [143]. Type data: holotype – WAM R27648, Kalumburu, WA [14° 18' S, 126° 30' E].

Diagnosis. Body size small to moderate (to 55 mm SVL) with long tail (2.5–2.7 × SVL). Gular fold absent, post-auricular fold weak to moderate, scapular fold moderate to strong. Granular scales in axilla, extending over arm onto neck to posterior edge of the scapular fold. Scales on outer rows of dorsolateral stripes have raised trailing edge in some individuals, particularly over shoulder, giving moderate demarcation between dorsal and lateral surfaces. Enlarged pale scales on sides tending to form vertical bars. Pre-cloacal pores 4; femoral pores 0.

Description of holotype. Female; 55 mm SVL; 128 mm tail length. A medium-sized *Diporiphora*, moderately gracile with long limbs and tail. One canine on either side of upper jaw. Gular, post-auricular and scapular folds absent. Dorsal scales strongly keeled, relatively large and homogenous, although band of smaller homogenous scales across back of head and neck. Longitudinal series of raised, but not enlarged, pale paravertebral and dorsolateral scales at the shoulder, not extending down dorsum. Scales on flanks homogeneous, although changing from small granular scales in axilla to small, non-granular scales on the posterior two-thirds of flanks. A few small pale spinose scales at back of head on each side, lacks spinose scales limbs on tail. Granular scales in axilla, extending over arm onto neck to posterior edge of the scapular fold. Ventral scales strongly keeled. Pre-cloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Six irregular dark brown squares (rather than transverse bands) between head and pelvis either side of a broad grey vertebral stripe, intersected by poorly defined, light brown dorsolateral stripes. Dark brown squares are narrower than the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Complex patterning on flanks; granular scales on flanks around arm are dark brown, extending posteriorly onto flanks that have speckled appearance due to seemingly random assortment of scale colours from white, cream, grey, light brown and dark brown; dark dorsal squares also extend as dark patches onto flanks. Lateral stripe between axilla and groin absent. Darker scales in axilla not extending up onto shoulder. Arms with faint dark banding. Banding on legs not well defined, with light bands narrower than dark bands. Dark bands on anterior third of tail, fading to unbanded light colouration for remainder of tail. Ventral surface cream with a few scattered fleck of light brown on ventrum, throat and head.

Figure 18. *Diporiphora margaretae*: a, adult male (NMV D73834), King Edward River, Kimberley, Western Australia (photo: J. Melville); b, holotype WAM R27648, Kalumburu, Western Australia.

Variation. 44–55 mm SVL; 110–135 mm tail length. Tail long, ranging from 2.5–2.7 × SVL. Gular fold always absent, post-auricular and scapular vary from weak to moderate. Low nuchal crest present. Spinose scale above tympanum, with 1–4 low spines on post-auricular fold. On dorsolateral row on neck, scales with posterior edges raised. Dorsal scales relatively homogeneous; an exception is the 2nd paravertebral row tending to be slightly enlarged. On flanks, keels of scales angled dorsally and posteriorly; flanks with scattered enlarged scales, tending to align vertically. Pre-cloacal pores 4; femoral pores 0.

Dorsal colour pattern variable. In patterned individuals, cream, grey, light brown to dark brown complex pattern with white dorsolateral stripes. Five or six irregular dark brown bands either side of a broad greyish vertebral stripe 3–5 scales wide. Granular scales on flanks around arm are usually dark brown, extending posteriorly onto flanks. Sides with speckled appearance due to scattered pale scales on enlarged scales on a dark background, often forming vertical rows. The dark bands on the dorsal surface do not extend laterally on the body and in most individuals the bands do not extend beyond the white dorsolateral stripes. In small heavily marked individuals, there is often a dark-edged pale lateral stripe. In plainer individuals, often adult males, dark transverse bands across the dorsum are either absent or faint. Lateral surfaces not as dark and speckled as for patterned individuals. No white markings on face, labial scales speckled with dark brown flecks. Banding on limbs not well defined, with light bands narrower than dark bands. Dark bands on anterior third of tail, fading to unbanded light colouration for remainder of tail. Ventral surface cream sometimes with a few scattered flecks of light brown on gular region and ventrum; occasionally several pairs of lines in gular region.

Distribution and ecology. Restricted to the far north Kimberley region, with records from the Anjo Peninsula and Sir Graham Moore Island in the extreme north, Kalumburu, Mitchell Plateau, Prince Regent River and Drysdale River National Parks, and on Mary Island.

This species has been recorded from Eucalyptus woodland, cane grass, triodia on sandstone and other rocky areas.

Comparison to other species. The distribution of *D. margaretae* overlaps with a number of other *Diporiphora* species, including *D. albilabris, D. bennettii*, *D. perplexa* sp. nov., *D. magna* and *D. pallida* sp. nov. *Diporiphora maragetae* differs from *D. magna* in having weak or absent post-auricular and scapular folds (as opposed to consistently strong folds), and having flanks that have a speckled or barred appearance due to scattered pale scales on a dark background. *Diporiphora margaretae* can be distinguished from *D. albilabris, D. bennettii* and *D. perplexa* sp. nov. in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw. *Diporiphora margaretae* differs from *D. pallida* sp. nov. in possessing a more gracile habitus with longer limbs and tail, lacking a gular fold and having granular scales in axilla.

Remarks. This species was originally described as a subspecies on *D. bilineata* (Storr, 1974) but was subsumed into *D. magna* without comment in Storr et al. (1983), despite having the largest difference in body size of any species pair within the *D. bilineata* species group. Genetic work, across multiple genes (Smith et al. 2011), demonstrated the distinctiveness of this species relative to *D. bilineata* and *D. magna*. Phylogenetic analyses support it being the sister species to *D. gracilis* sp. nov. (fig. 1c).

Diporiphora gracilis sp. nov.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:F3BB16E0-259E-4396-AD68-FFE06A0FE624

Common name. Gracile two-lined dragon.

Figure 19, Tables 3, 4

Holotype. WAM R177291 (formerly NMV D75540) (adult male), Fairfield-Leopold Downs Road, south of Gibb River Road, WA (17° 29' 37.0" S, 125° 2' 17.7" E). Collected by P. Oliver on 2 November 2013.

Paratypes. NMV D75541 (adult females), as for holotype; NMV D73901 (adult male), as for holotype; WAM R163503 (female) and WAM R163504 (male), Mornington Station, WA (17° 30' 23" S, 126° 02' 07" E); WAM R177952 (formerly NMV D75542) (adult female), as for holotype.

Diagnosis. Body size moderately long (to 61 mm SVL) with elongate and gracile body shape and very long tail (to 3 × SVL). Gular fold absent, post-auricular and scapular folds weak. Granular scales in axilla, extending over arm to scapular fold. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

Description of holotype. Male; 57 mm SVL; tail length 165 mm. A medium-sized gracile *Diporiphora*, with long limbs and a very long tail. One canine on either side of upper jaw. Gular fold absent; post-auricular and scapular folds weak. Dorsal scales on torso strongly keeled, parallel to midline and homogenous; heterogeneous scales on head with wide band of smaller scales across back of head and neck. Low nuchal crest of ~8 scales. Granular scales in axilla, extending over arm to the weak scapular fold. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Lacks spinose scales on limbs or tail. Ventral scales weakly keeled on head and throat, strongly keeled on body. Pre-cloacal pores 4; femoral pores 0.

Dorsal colour greyish-brown without patterning. Dorsolateral and vertebral stripes absent. Dark transverse bands between head and pelvis absent. Head relatively plain, labials similar colour to rest of head and lacking pale line between eye and ear; lateral portions of snout paler than dorsal surface of snout. Dark smudge on posterior of tympanum absent. Granular scales on axilla dark brown, posterior two-thirds of flanks same colour as dorsal surface. Lateral stripe between axilla and groin absent. Dark patch in axilla, not extending up onto shoulder. Faint banding on hind limbs; tail plain without banding. Arms lack dark banding. Ventral surface cream with no patterning, lower labials faintly stippled.

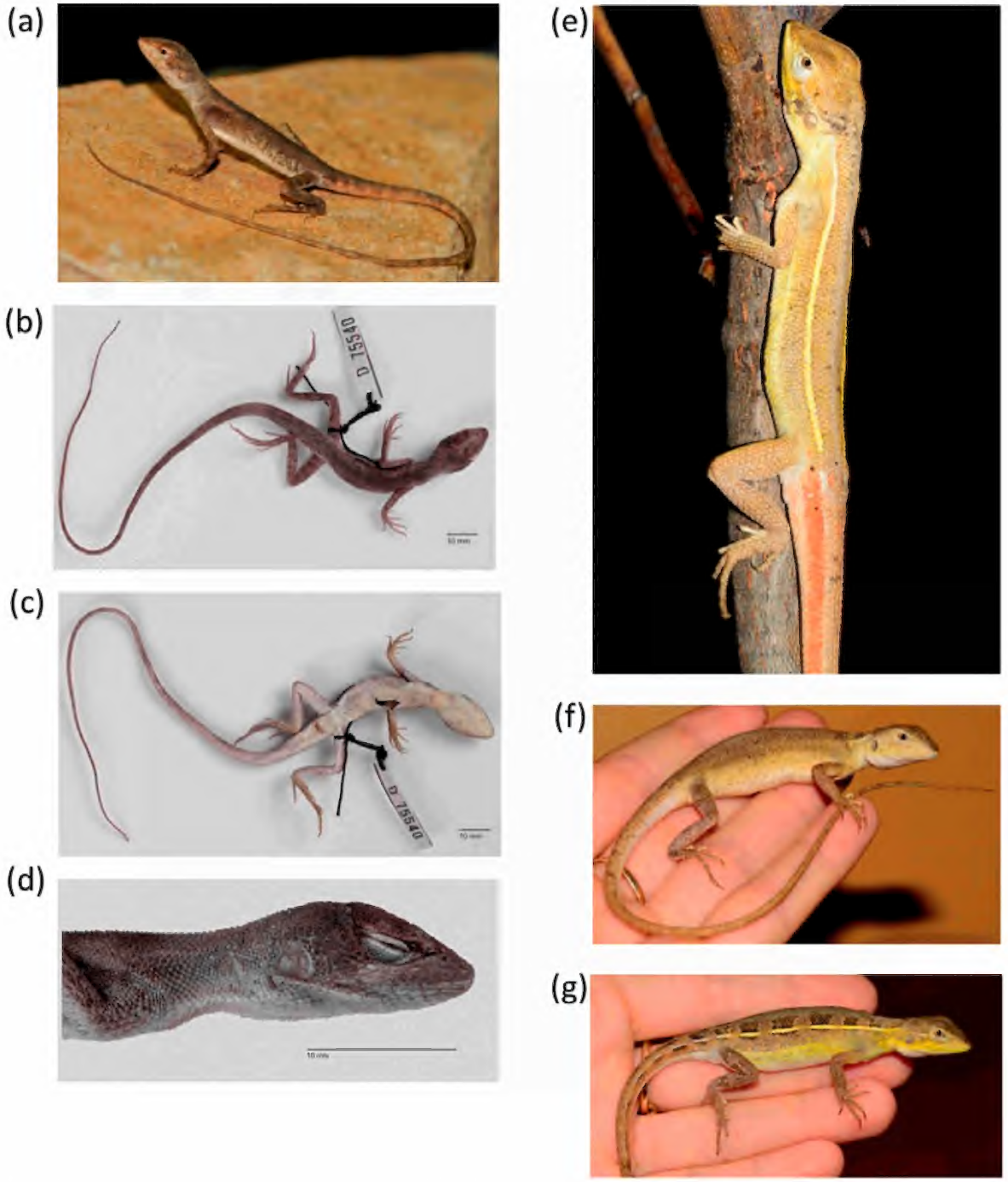

Figure 19. *Diporiphora gracilis* sp. nov. Images of holotype (WAM R177291, formerly NMV D77540), Fairfield-Leopold Downs Road, south of Gibb River Road, Western Australia: a, in life (photo: J. Sumner); b, c, d, dorsal, ventral and, lateral (head) views. Pattern variation (individuals from Mornington Station, Western Australia: e, adult male with breeding colour; f, gravid female (plain); g, gravid female (patterned) (photos: Melissa Bruton, Australian Wildlife Conservancy).

Variation. 52–61 mm SVL; 140–185 mm tail length. Very long tail, ranging from 2.7–3.0 × SVL. Gular fold always absent, post-auricular fold weak or absent, and scapular fold weak. At most, a single small spinose scale above tympanum and one on post-auricular fold. Dorsal scales homogeneous. Presence of outer raised trailing edge of scales on outer row of dorsolateral stripes variable – usually absent in more plain individuals but present in those with strong patterning, providing weak demarcation between dorsal and lateral surface. Gulars smooth. Pre-cloacal pores 4; femoral pores 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, dark brown bands offset each other to either side of a broad greyish vertebral stripe, pale well-defined dorsolateral stripes (approximately two scales wide) that extend from back of head to hind legs, where stripes continue as broken stripes down a third of the tail. Dark dorsal cross-bands continue beyond dorsolateral stripes to a narrow pale lateral stripe. Below lateral stripes is plain with start of cream ventral colour. No patterning on head, lacks pale stripe between eye and ear. Faint banding on limbs and banding on anterior third of tail. In plain individuals, there is no patterning on body or head, including no dorsolateral or vertebral stripes. In these plain individuals, granular scales in axilla are dark brown and in life have a well-defined black spot on sides and a greenish-yellow hue to body. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on limbs. Ventral surface cream, without markings. In life, males with breeding colouration have a well-defined black spot on sides, a greenish-yellow hue to body and a pink flush on the tail.

Etymology. Named for the gracile body shape, with noticeably long and slender body, limbs and tail. Used as a noun in apposition.

Distribution and ecology. Restricted to the south-western Kimberley region (fig. 14). Currently only known from two locations, the type location on the Fairfield-Leopold Downs Road and further east on Mornington Station, approximately 80 km apart.

Diporiphora gracilis sp. nov. appears to be a grassland specialist, occupying savannah grasslands on clay soils associated with the floodplain of the Lennard River. More collecting is required to determine how far the distribution of this species extends and whether it is only associated with grasslands on clay soils.

Comparison with other species. The distribution of *D. gracilis* sp. nov. overlaps numerous other *Diporiphora* species. The distribution of *D. pindan* overlaps with *D. gracilis* sp. nov. but they appear to occupy different habitats (*D. gracilis* sp. nov. in grasslands on floodplains; *D. pindan* in shrubs and spinifex). *Diporiphora pindan* can be distinguished from *D. gracilis* sp. nov., with the latter lacking a well-defined white stripe between eye and ear, having strongly keeled dorsal scales where keels form longitudinal ridges running along torso and having a very long tail in proportion to body size. Differs from *D. magna* in lacking strong post-auricular and scapular folds, and having a more gracile habitus. Differs from *D. lalliae* in lacking gular fold and possessing granular scales in axilla. Differs from *D. albilabris*, *D. bennettii*, *D. sobria* and *D. perplexa* sp. nov. in lacking femoral pores, lacking a gular fold and having single canines on each side of the upper jaw.

Remarks. This species is sister to *D. margaretae* from the northern Kimberley, both of which form a Kimberley endemic lineage compared to the next closely related species, *D. lalliae* and *D. magna*, which both extend across the Kimberley and NT to just inside the Queensland border.

Diporiphora gracilis sp. nov. was first collected on Mornington Station in 2004. The collection of further individuals by J. Melville that had tissues taken establishes this species' distinctiveness, and the morphology of these specimens is shared by the two Mornington specimens.

Diporiphora granulifera sp. nov.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:B6B3DAEB-9D8E-4D5A-A53B-04BF6962C3B1

Common name. Granulated two-lined dragon.

Figure 20, Tables 3, 4

Holotype. QM J96362 (formerly NMV D74060) (adult male), Downs Road, 2 km from Barkly Highway, Queensland (20.3714° S, 139.1529° E). Collected by K. Smith in October 2005.

Paratypes. NMV D74047 (adult female), Lawn Hill Station, Queensland (18.6536° S, 138.5653° E); NMV D74054 (adult male), Carpentaria Highway, west of Burketown, Queensland (18.0242° S, 139.0077° E); NMV D74062 (adult male), Downs Road, 2 km from Barkly Highway, Queensland (20.3717° S, 139.1525° E).

Diagnosis. Medium-large species (to 68 mm SVL) with a very long tail (>2.5 × SVL). Gular fold absent, post-auricular fold weak and scapular fold strong. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck anterior to scapular fold small and slightly granular. Outer scale row in dorsolateral stripes have raised posterior edge, particularly over shoulder, giving strong demarcation between dorsal and lateral surfaces. Pre-cloacal pores 4–6 (usually 4); femoral pores 0.

Description of holotype. Male; 65 mm SVL; 176 mm tail length. Medium-large *Diporiphora*, moderately gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent. Post-auricular and scapular folds strong. Dorsal scales strongly keeled, relatively homogenous. Longitudinal series of raised but unenlarged pale dorsolateral scales at the shoulder, extending down posteriorly along dorsum to base of tail. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but not granular scales on the posterior two-thirds of flanks. Lacking cluster of spinose scales at rear of head on the post-auricular fold, lacks spinose scales limbs or tail. Small granular scales in axilla, extending up over shoulder and along under full extent of the scapular fold. Scales on sides of neck anterior to scapular fold small and slightly granular. Ventral scales strongly keeled. Pre-cloacal pores 6; femoral pores 0.

Dorsum light brown with little patterning. Faint broad grey vertebral stripe; well-defined cream dorsolateral stripes running from back of head to base of tail and associated with

raised but not enlarged longitudinal scales. Dark transverse bands absent. Head relatively plain with little patterning; labials similar colour to rest of head, although posterior third paler than anterior; poorly defined, faint pale stripe from eye to top of ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown then transition posteriorly into cream, grey and light brown with little patterning; flanks have darker dorsal patterning above and pale cream ventrally; flecked with a few light brown scattered scales. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up over shoulder and down full length of scapular fold. Arms lack dark banding. No patterning on legs, faint banding on anterior third of tail with dark bands wider than pale bands. Ventral surface cream with no patterning.

Figure 20. *Diporiphora granulifera* sp. nov.: a, in life, Lawn Hill, Queensland (photo: S. Wilson). b, c, d, dorsal, ventral and lateral (head) views of holotype QM J96362 (formerly NMV D74060) Downs Road, 2 km from Barkly Highway, Queensland.

Variation. 44–68 mm SVL; 121–179 mm tail length. Very long tail, ranging from 2.7–3.0 × SVL. Gular fold always absent, post-auricular fold weak to present, scapular fold strong, extending onto edges of ventrum. In some animals, enlarged scales on post-auricular fold has an enlarged cluster of scales at the ventral extent but without a single spinous scale. Pre-cloacal pores variable from 4–6 (usually 4); femoral pores always 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, approximately 6–8 dark brown bands slightly offset to each other on either side of a broad undefined greyish vertebral stripe. Banding extends onto tail, fading out half way down tail. Well-defined pale dorsolateral stripes, running from back of head to base of tail and becoming interrupted by banding pattern of tail. Flanks have a faint, poorly defined light brown lateral stripe, with darker dorsal patterning above and pale cream below. Flanks flecked with a few light brown scattered scales. In more plain individuals, pale dorsolateral stripes from neck onto base of tail. Granular scales in axilla are dark brown; flanks cream, grey or light brown with little patterning. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on limbs. Ventral surface cream, usually plain but some individuals have faint dark flecking on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a large black patch in axilla extending on to shoulder and some having a pink flush on base of tail.

Etymology. Named for the extensive granulated scales on sides of body.

Distribution and ecology. Restricted to the far north-west Gulf of Carpentaria region of Queensland. More collecting is required to determine how far east this species extends and whether it extends west into the NT. A habitat generalist occurring in tropical savannah woodlands and grasslands. Has been observed perching on low vegetation, rocks or termite mounds.

Comparison to other species. The distribution of *D. granulifera* sp. nov. contacts a number of other *Diporiphora* species in the western Gulf of Carpentaria region. Very similar morphologically to *D. carpentariensis* sp. nov. and it remains unclear whether they come into contact in the central Gulf of Carpentaria region, but can be distinguished from this species in lacking or having weak spinose scales on the post-auricular fold and in having granular scales extending anteriorly to the scapular fold, with scales on the sides of neck more homogenous and outer scale row in dorsolateral stripes having raised trailing

edge, particularly over shoulder, giving strong definition between dorsal and lateral surface. Differs from *D. magna* in having granular scales extending over shoulder and along scapular fold, slightly onto ventral surface of neck. Differs from *D. lalliae* in lacking a gular fold. Can be distinguished from *D. sobria* in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw.

Remarks. Although very similar morphologically to *D. carpentariensis* sp. nov., the genetic analysis of Smith et al. (2011) across multiple genes distinguished these two species as divergent lineages that are not each other's closest relatives. It remains to be determined if these two species contact in the central Gulf of Carpentaria region.

Recent unpublished phylogenomic research using single-nucleotide polymorphisms shows that *D. granulifera* sp. nov. is highly divergent and genetically distinguishable from *D. magna* (as defined above) (J. Fenker, unpublished data). However, there is evidence of gene flow and mtDNA introgression between these two species in areas of contact, including along the Barkly Highway, Queensland. The holotype (QM J96362), which was included in this genomic analysis, was confirmed as being *D. granulifera* sp. nov. and is not a hybrid animal, with no evidence of genomic contribution from *D. magna*.

Diporiphora granulifera sp. nov. contributes to a small number of endemic lizard and frog species from the Gulf of Carpentaria region, including *Cryptoblepharus zoticus* Horner, *Oedura bella* Oliver and Doughty and *Litoria electrica* Ingram and Corben. Further genetic and morphological work on species that span the Gulf of Carpentaria area may reveal further interesting phylogenetic patterns in this poorly sampled region.

Diporiphora carpentariensis sp. nov.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:6795AD24-03D8-4E4E-9FD8-4757AEE964C5

Common name. Gulf two-lined dragon.

Figure 21, Tables 3, 4

Holotype. QM J88197 (adult male), Littleton National Park, northern Queensland (18.2243°S, 142.7489 E). Collected by E. Vanderduys on 20 November 2008.

Paratypes. NMV D74080 (adult female), Mt Turner Road, 5 km north of Gulf Development Road, Queensland (18.2692° S, 143.3647° E); NMV D74079 (adult male), Mt Turner Road, 20 km north of Gulf Development Road, Queensland (18.2733° S, 143.3656° E); NMV D74076 (adult female), road to Strathmore, 3 km north of Gulf Development Road, Queensland (18.1783° S, 142.8844° E); NMV D74068 (adult male), Bourke Development Road, 25 km NE of Karumba turnoff, Queensland (17.3931° S, 141.3989° E).

Diagnosis. Moderately large body size (to 68 mm SVL), with adult males with very long tails (to 3 × SVL) and females with shorter tails (to 2.3 × SVL). Gular fold absent, post-auricular fold weak to strong, scapular fold strong. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck in anterior to scapular fold small but not granular. Outer scale row in dorsolateral stripes lack raised trailing edge, without strong delimitation between dorsal and lateral surface. Pre-cloacal pores 4 or 5 (usually 4); femoral pores 0.

Description of holotype. Male; 62 mm SVL; 185 mm tail length. Medium-large *Diporiphora*, gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent, post-auricular fold weak and scapular fold strong, extending onto edges of ventrum. Dorsal scales strongly keeled, relatively homogenous. Longitudinal series of raised but not enlarged pale paravertebral and dorsolateral scales at the

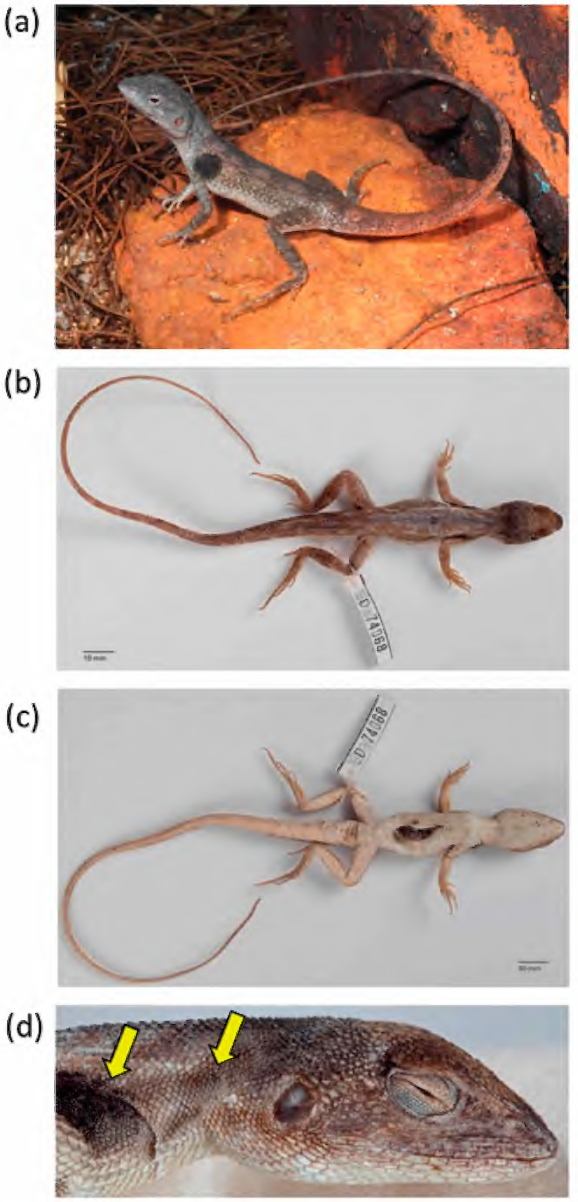

Figure 21. *Diporiphora carpentariensis* sp. nov. Image of holotype (QM J88197), Littleton National Park, northern Queensland, a, in life (photo: E. Vanderduys); b, c, d, dorsal, ventral and lateral (head) view of paratype NMV D74068.

shoulder, extending down back to base of tail. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Cluster of small spinose scales on post-auricular fold with one cream-coloured spine being clearly larger than the others. Lacks spinose scales on limbs or tail. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck, anterior to scapular fold small but not granular. Ventral scales strongly keeled. Pre-cloacal pores 5 (2 on right; 3 on left); femoral pores 0.

Dorsum light brown with little patterning. Faint, broad grey vertebral stripe; well-defined cream dorsolateral stripes running from back of head to base of tail, associated with raised but not enlarged longitudinal scales. Dark transverse bands absent. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown then transition posteriorly into cream, grey and light brown without patterning; flanks have darker dorsal patterning above and pale cream ventrally; flecked with a few light brown scattered scales. Lateral stripe between axilla and groin absent. Dark patch in axilla, associated with granular scales, continues up over shoulder and down full length of scapular fold. Banding on limbs absent; faint banding on anterior third of tail, with dark bands narrower than the light bands. Ventral surface cream with no patterning.

Variation. 52–65 mm SVL; 118–187 mm tail length. Very long tail, ranging from 2.1–3.0 × SVL. Tail length appears to be sexually dimorphic with adult male tails ranging from 2.7–3.0 × SVL, while adult female tails ranging from 2.1–2.3 × SVL. Gular fold always absent, post-auricular fold weak to present, scapular fold strong, extending onto edges of ventrum. In some animals, a cluster of small spinose scales on post-auricular fold has an enlarged scales that is not obviously spinous. Pre-cloacal pores variable from 4–5 (usually 4); femoral pores always 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, eight or nine dark brown bands slightly offset to each other on either side of a broad undefined greyish vertebral stripe. Banding extends onto tail, fading out halfway down tail. Well-defined pale dorsolateral stripes, running from back of head to base of tail and becoming interrupted by banding pattern of tail. Flanks have faint poorly defined light brown lateral stripe, with darker dorsal patterning above and dark background colour extending slightly below stripe. Flanks flecked with a few light brown scattered scales. In more plain individuals, pale dorsolateral stripes from neck onto base of tail. Granular scales in axilla are dark brown or black, flanks cream, grey, light brown with little patterning. No white markings on head, labial scales speckled with light brown flecks. Faint or no banding on legs and tail. Ventral surface cream, usually plain but some individuals have faint dark flecking on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a large back patch in axilla extending onto shoulder but not anteriorly of the scapular fold, and some males have a pink flush on base of tail.

Etymology. Named for the region in which this two-lined dragon occurs on the Gulf of Carpentaria.

Distribution and ecology. *Diporiphora carpentariensis* sp. nov. is restricted to the far north-east Gulf of Carpentaria region of Queensland at the western extent of Cape York Peninsula. More collecting is required to determine whether this species extends further west into the Gulf of Carpentaria region. It appears to be habitat generalist, occurring in tropical savannah woodlands and grasslands. Little is known about this species and further field-based work is needed to determine the extent of its distribution and its ecological requirements, habitat preferences and behaviour.

Comparison to other species. The distribution of *D. carpentariensis* sp. nov. overlaps a number of other *Diporiphora* species in the Gulf of Carpentaria region. Very similar morphologically to *D. granulifera* sp. nov. and remains unclear whether they contact in the central Gulf of Carpentaria region but can be distinguished from this species in having spinose scales on the post-auricular fold, with a single spine clearly larger than the others, and in lacking granular scales extending anteriorly from the scapular fold, and outer scale row in dorsolateral stripes lack raised trailing edge without a strong demarcation from the dorsal to lateral surface. *Diporiphora carpentariensis* sp. nov. differs from *D. jugularis* in having a strong scapular fold, granular scales in axilla that extend over shoulder and along scapular fold, scales on flanks relatively homogeneous and lacking a black gular band or black spot on sides of neck. *Diporiphora carpentariensis* sp. nov. can be distinguished from *D. australis* in lacking a gular fold and having granular scales in axilla that extend over shoulder and along scapular fold.

Remarks. This species has previously been identified as *Diporiphora bilineata*. It is probable that animals previously identified as *D. bilineata* on Cape York Peninsula actually comprise two species: *D. carpentariensis* sp. nov. and *D. jugularis*. Phylogenetic work (Smith et al., 2011) clearly shows that this species in unrelated to either *D. bilineata* or *D. jugularis* (fig. 1).

(d) Arid zone species group

Content:

D. adductus Doughty, Kealley and Melville, 2012
D. ameliae Emmott, Couper, Melville and Chapple, 2012
D. linga Houston, 1977
D. paraconvergens Doughty, Kealley and Melville, 2012
D. pindan Storr, 1980
D. valens Storr, 1980
D. vescus Doughty, Kealley and Melville, 2012
D. winneckei Lucas and Frost, 1896
D. pallida sp. nov.

Diagnostic characters for group in north-western Kimberley:

- one canine tooth on each side of upper jaw
- axilla granular scales absent
- lateral dark spot absent
- femoral pores absent.

Remarks

The arid zone species group is widely distributed across arid WA (Couper et al., 2012; Doughty et al., 2012a), with highest species diversity in the Pilbara region but extending north to the southern Kimberley (*D. pindan*) and east into the arid interior (*D. paraconvergens*), crossing into South Australia and the NT. However, *D. pallida* sp. nov. is from the Mitchell Plateau (fig. 22), north-western Kimberley, more than 450 km north of the nearest member of this species group (*D. pindan*). *Diporiphora pallida* sp. nov. expands the bioclimatic and distributional limits of the arid zone species group. Key characters in distinguishing the arid zone species group from the other species groups in northern Australia is the number of canine teeth on each side of the upper jaw combined with the absence of granular scales in the axilla. In addition to these characters, in the Kimberley region this species group can be distinguished from *D. lalliae* (a member of the *D. bilineata* species group) by species-specific characters: the lack of a gular fold for *D. pindan* and a short tail for *D. pallida* sp. nov.

Diporiphora pallida sp. nov.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:7967A170-9260-40F9-A895-D5C5041E4729

Common name. Pale two-pored dragon.

Figure 22, Tables 3, 4

Holotype. WAM R177292 (formerly NMV D73853) (adult male), Mitchell Plateau, WA (14° 49.45' S, 125° 42.12' E). Collected by J. Melville on 12 September 2005.

Diagnosis. Small body size (to 46 mm SVL), short tail (2.0 × SVL), robust head and prominent brow above eye. Gular fold strong, post-auricular fold weak, scapular fold present. Single canine in upper jaw, no granular scales in axilla. Pre-cloacal pores 2; femoral pores 0.

Description. Male; 46 mm SVL; 91 mm tail length. Small *Diporiphora*, robust head with relatively short tail (~2.0 × SVL) and limbs. One canine on either side of upper jaw. Gular fold strong, post-auricular fold weak and scapular fold present. Prominent ridges above eye, extending along canthal ridge to dorsal corner of nasal scale, with short tapered snout. Dorsal scales strongly keeled and homogenous, running parallel to the midline. Scales on flanks homogeneous, keels angled posteriorly and dorsally. One small white spinose scale at back of head sitting on ventral end of post-auricular fold. Lacks spinose scales on limbs or tail. Small scales in axilla but not granular. Ventral scales strongly keeled. Pre-cloacal pores 2; femoral pores 0.

Dorsum relatively plain with little patterning. Broad (~4 scales wide) greyish indistinct vertebral stripe and broad yellow-cream dorsolateral stripes (~3 scales wide) running from back of head to base of tail; dorsolateral stripes continuous from head to mid-dorsum, and from there broken into sections by background colour. Dark transverse bands absent. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Flanks pale without patterning. Lateral stripe between axilla and groin absent. Dark patch in axilla absent. Banding on limbs and tail absent. Ventral surface cream with no patterning.

Variation. This description is based on a single specimen collected on the Mitchell Plateau, thus the variation in this species is unknown.

Etymology. Named for the pale appearance of this species in life. Used as an adjective.

Distribution and ecology. Based on a single animal, *D. pallida* sp. nov. occurs on the Mitchell Plateau in the northwest Kimberley. This animal was found perched in spinifex grass on a rocky outcrop (pictured in fig. 22). Little is known of this species but it appears to be associated with spinifex grasses on rocky substrates.

Comparison to other species. Unlike other dragons found in the northwest Kimberley, *D. pallida* sp. nov. appears to be a habitat specialist in spinifex grasses and has a distinctive morphology. Its distribution overlaps with *D. margaretae*, but differs in having a gular fold. It also differs from *D. albilabris*, *D. bennettii* and *D. perplexa* sp. nov. in having a single canine on either side of upper jaw and further differs from *D. albilabris* in lacking femoral pores.

Remarks. Genetic analyses indicate that this species is not related to other *Diporiphora* species in the Kimberley but instead belonging to the arid zone species group containing other spinifex specialist species (e.g. *D. linga* and *D. winneckei)*, which occur in arid central Australia. In mtDNA phylogenetic analysis, this species was resolved as the sister to *D. paraconvergens*, but this relationship was not strongly supported (fig. 1). *Diporiphora pallida* sp. nov. can be readily distinguished from *D. paraconvergens* by dorsal scales that run parallel to the midline (vs. converging) and by having a short tail (vs. very long). Based on genetic results and morphological distinctiveness we feel confident that this a new species for the Kimberley region, joining *D. convergens* as another *Diporiphora* species known only from the holotype. Further sampling is required to gain a better understanding of the ecology, biology and evolutionary relationships of this little-known species.

Discussion

Our study provides the first comprehensive taxonomic treatment of *Diporiphora* species across northern Australia since Storr's revision in 1974. Using an understanding of relationships based on genetic data and a re-examination of newly collected and historical specimens, we describe five new species, raise a further two taxa to full species status and redefine six existing species. This work significantly increases the species diversity of *Diporiphora*, and agamid lizards, in the AMT.

Diporiphora species occur in most habitats in the AMT and are one of the most common and abundant lizards in the tropical savannah woodlands and grasslands. The Australian tropical savannah is one of the largest and most intact in the world (Bowman et al., 2010; Laver et al., 2018), and is globally significant. Despite this importance, we are only beginning to document the true species diversity of many vertebrate groups (e.g. Afonso Silva et al., 2017; Doughty 2011; Doughty et al.,

2012b, 2018; Laver et al., 2018; Melville et al., 2018; Pepper et al., 2011; Potter et al., 2012). With these recent studies and our taxonomic treatment documenting lizard diversity patterns in geckos, skinks and agamids, we can start to look for concordant patterns of diversity between these lineages. Three clear patterns are apparent across these major lineages: (1) greater species diversity in the northern extent of the AMT, particularly the Kimberley region; (2) fewer and more widely distributed species in southerly portions of the AMT; and (3) consistent major biogeographic breaks across terrestrial vertebrate groups.

A consistent pattern in studies investigating phylogeographic structuring and species diversity across the AMT is a north–south gradient of diversity in lizard lineages. In the northern parts of the AMT, species diversity is greatest, with particular diversity hotspots in the north-western Kimberley and Arnhem Land regions (e.g. Powney et al., 2010). In addition to higher species diversity, there are higher numbers of short-range endemic species in these northern hotspots. For example, in the *Oedura* geckos of the AMT, genetic evidence suggests that microendemism and diversity is highest in the northern AMT high-rainfall regions (Laver et al., 2018), while the most widespread lineages occur in the more southerly boundary between the AMT and Australian arid zone. Similarly, in *Diporiphora* the highest species diversity is in the Kimberley, with three lineages (*D. bilineata, D. bennettii* and arid zone species groups) occurring in the region. Each of these species groups contain more than one species in the Kimberley, with all four species from the *D. bennettii* species group occurring in the region, including two locally endemic (*D. bennettii* and *D. albilaris*). In contrast, the southern region of the AMT has fewer *Diporiphora* species but they have broad east–west distributions (*D. sobria, D. magna* and *D. lalliae*), with the later of these encroaching into the Australian arid zone. This north–south pattern of species diversity, which appears across multiple groups, has been attributed to an aridity gradient, climate stability or instability, and historical refugia in mesic areas (Afonso Silva et al., 2017; Laver et al., 2018; Palmer et al., 2013). The hypothesis that the presence of rocky refugia drives patterns of diversity is supported by higher diversity along the barrier ranges in the southern Kimberley (Doughty et al., 2018; Oliver et al., 2014, 2016).

In addition to documenting greater species diversity in *Diporiphora*, our work also demonstrates that there is high diversity in body size and ecology within the Kimberley region, with large and small sympatric species within each species group and with ecological variation. In the *D. bennetti* species group, there are two rock-specialist species, one large (*D. perplexa* sp. nov.) and one small (*D. bennettii*), and a smaller generalist woodland species (*D. albilabris*). Similar body size divergence in sympatric rock-dwelling *Gehyra* species has been documented in the Kimberley (Moritz et al., 2018; Oliver et al., 2016). In the *D. bilineata* species group, there is a generalist woodland species (*D. margaretae*) with smaller body size in the northern Kimberley and a gracile species found in grasslands on river floodplains in the southern Kimberley (*D. gracilis* sp. nov.), although it is unlikely these species are sympatric. These patterns suggest that more than

Figure 22. *Diporiphora pallida* sp. nov. Images of holotype (WAM R177292, formerly MNV D73853), Mitchell Plateau, Western Australia: a, in life (photo: J. Melville); b, c, dorsal and ventral views; d, collection location.

mesic refugia and aridity gradients are shaping diversity in Kimberley *Diporiphora* species, and that ecological and morphological diversification through processes other than evolutionary drift may drive diversity patterns. Regardless of the mechanisms, there is a clear pattern for high species diversity in the Kimberley, with more widespread species within the AMT appearing to arise within these Kimberley species groups.

In the more southerly regions of the AMT, this diversity in body size is not apparent in *Diporiphora*. Across the east–west span of the AMT, past climatic fluctuations and aridity gradients have probably shaped species diversity. A number of major biogeographic breaks have been identified in different lizard lineages, several which appear to be relatively consistent across groups (e.g. Noble et al., 2018). Genetic differentiation across two biogeographic barriers – the Carpentaria Gap in the Gulf of Carpentaria region of Queensland and the Ord River region between the Kimberley region and the Top End of the NT – has been well documented across numerous taxa (Catullo et al., 2014; Noble et al., 2018; Potter et al., 2012), including agamid lizards (see Pepper et al., 2017). In *Diporiphora*, the divergence across the Carpentaria Gap appears to be most dramatic. For example, in the *D. bilineata* species group, the distributions of *D. bilineata, D. magna* and *D. granulifera* sp. nov. appear to truncate at the western portions of the Carpentaria Gap, while *D. carpentariensis* sp. nov. is to the east of this biogeographic barrier. In addition, the *D. australis* species group is only found to the east of the Carpentaria Gap (see Edwards and Melville, 2010, 2011). The divergence of species across the Gulf of Carpentaria region has been attributed to increased aridity in these regions compared to adjacent topographic uplands (Pepper et al., 2017). It remains unclear as to whether AMT *Diporiphora* species groups have a distributional gap in the Gulf of Carpentaria region of Queensland, as is currently suggested by maps, or is this due to a lack of sampling and records in this region. Further field-based research is needed to fully elucidate the distributions of *Diporiphora* species across this biogeographic barrier.

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A redescription of *Eulimnadia rivolensis* (Brady, 1886) (Branchiopoda: Spinicaudata: Limnadiiidae), and its transfer to *Paralimnadia*

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Abstract

Timms, B.V. 2019. A redescription of *Eulimnadia rivolensis* (Brady, 1886) (Branchiopoda: Spinicaudata: Limnadiiidae), and its transfer to *Paralimnadia*. *Memoirs of Museum Victoria* 78: 57–64.

Eulimnadia rivolensis occurs across the southern Australian mainland and Tasmania but has not been collected in Victoria since 1910 and in south-east South Australia since 1975, where its former habitat has been destroyed. *E. rivolensis* is redescribed from syntype material and transferred to *Paralimnadia*. This species lacks a subcercopod spine and has other less characteristic features of *Paralimnadia*. *Eulimnadia palustera* Timms, 2015 is a junior synonym based on egg morphology and some characteristics of the telson.

Keywords

Subcercopod spine, cercopods, resting eggs, *Eulimnadia palustera*

Introduction

The taxon *Eulimnadia rivolensis* Brady, 1886, of southern Australia has had a chequered history. It was first applied to specimens from the Rivoli Bay environs in south-eastern South Australia, but the description is only of the carapace shape, which is now known to vary with age and habitat (Rogers et al., 2012; Straškraba, 1965), and the illustration could apply to many limnadiid species. Next, the name was used without any justification by Spencer and Hall (1896) for specimens supposedly from Central Australia. Sayce (1903) published some details of the morphology of *E. rivolensis* and provided more accurate drawings, basing his observations on specimens from Victoria and South Australia. Sayce's (1903) Onkaringa (Onkaparinga) Creek site was erroneously recorded as being in Central Australia, but it drains the eastern Adelaide Hills, and so this error introduces possible inaccuracies in distribution. Sayce (1903) suggested, without any evidence, that *E. rivolensis* may be synonymous with *Limnadia sordida*, which at that time was also poorly defined. Thus, New South Wales, the habitat of *L. sordida*, was added to the supposed distribution. This synonymy was perpetuated by Dakin (1914), who noted its occurrence in south-western Western Australia, and Henry (1924), except that *L. sordida* was moved to *Eulimnadia*. To add to the confusion, Daday (1925) retained the specific epithet *rivolensis* but transferred it to *Limnadia*. This was followed by Richter and Timms (2005), based on figures in Sayce (1903), and Gurney (1927) because neither recorded a subcercopod spine, a defining feature of *Eulimnadia* (Martin, 1989). Importantly, the species epithet was hidden in the synonymy, so its possible existence was not acknowledged in a recent review of Australian *Eulimnadia* (Timms, 2016a).

In 2015, I described *Eulimnadia palustera* from south-west Western Australia, which shares some features with Sayce's version of *E. rivolensis*, then thought to be *L. sordida*. Given that egg morphology in limnadiids is useful in distinguishing species (Belk, 1898; Rabet, 2010; Rogers et al., 2012; Timms, 2016a, 2016b), a comparison of the eggs from the few collections labelled *E. rivolensis* in the NMV and AM suggest a close similarity between the two species. In summary, there is uncertainty over the validity of *E. rivolensis* and *E. palustera*, to what species they are related and, indeed, to which genus they belong. Fortunately, there is enough material in the Australian Museum and National Museum Victoria to find solutions to these uncertainties. One subsidiary aim is to accurately plot the distribution of these species.

Material and methods

Drawings were made using a Wild M5 dissection microscope equipped with a camera lucida. Body measurements were made by placing a template marked in 0.5 mm spacings underneath the specimen at magnifications of 10–40 × and distance was estimated to the nearest half division. Accuracy is deemed to be ± 0.25 mm.

Eggs were prepared as detailed in Timms and Lindsay (2011) and studied on a Zeiss Evo LS15 Scanning Electron Microscope using a Robinson Backscatter Detector.

Terminology of the claspers of the Diplostraca follows Kaji et al. (2014): the hand (or palm) is composed of endites IV

and V; its thumb (or gripping knob) is derived from endite IV, the small palp from endite IV and the large palp from endite V; and the finger is derived from endite VI (or endopod).

Other abbreviations used in the text: AM = Australian Museum; BMNH = British Museum of Natural History; NMV = National Museum Victoria; SAM = South Australian Museum; WAM = Western Australian Museum.

Results

Taxonomy

Diplostraca Gerstaecker, 1866
Spinicaudata Linder, 1945
Limnadiidae Baird, 1849
***Paralimnadia* Sars, 1896, emend Rogers et al., 2012.**
***Paralimnadia rivolensis* Brady, 1886**

Figures 1–4

Eulimnadia rivolensis Brady, 1886: 86–67, fig. D. — Simon, 1886: 456 (list); Spencer and Hall, 1896: 238; Sayce, 1903: 245–246 (text), 248 (synopsis), pl. 32; Wolf, 1911 (list); Dakin, 1914: 295 (list), 300 (text); Gurney, 1927: 60–61, fig. 1A.

Limnadia rivolensis — Daday, 1925: 150 (key), 173–175, fig. 121; Webb and Bell, 1979: 243 (text), table 1; Richter and Timms (text): 348.

Eulimnadia palustera Timms, 2015: 447–449, fig. 6. **New synonym**

Lectotype. *South Australia*, hinterland of Rivoli Bay, R. Tate, date unknown but before 1886, BMNH 1890.2.1.9. Male 9.0 mm long and 6.0 mm high.

Paralectotypes. *South Australia*, hinterland of Rivoli Bay, R. Tate, date unknown but before 1886, BMNH 1890.2.1.10. Male 8.9 mm long and 5.5 mm high; Rivoli Bay, freshwater swamps, 11 November 1882, collector unknown, 4 males, 1 female, NMV J14426.

Comment. Because the Brady collection in the National Museum Victoria is labelled from Rivoli Bay and has a date that aligns with the approximate date of collection of the lectotype, I believe the two are the contemporaneous. Hence, the collection NMV J14426 are herein designated as paralectotypes, which is convenient given there are no females or eggs among the original syntypes in the British Museum of Natural History.

Other material. *Northern Territory*: Central Australia, 3 males, 5 females, from Sayce collection but no further data, NMV J54016; *South Australia*; Lake Robe, nearby puddle, Margaret Brock, 23 September 1975, 3 males, 1 female, SAM C12297; Snake Lagoon, Kangaroo Island, South Australia, 24 August 1981, D.J. Williams, 4 males, 2 females, SAM C12296; *Tasmania*: no site recorded, R.W. Davis, 18 October 1969, 4 males, 2 females, NMV J46599; 4 km north of Campbelltown, 41.93° S, 147.5° E , 24 November 1963, J. Wilson, 1 male, 2 females, AM P55663; 4 km north of Campbelltown, 41.93° S, 147.5° E, 20 March 1964, J. Wilson, 7 males, 10 females, AM P55640; 1 female, AM P98988; 1 male, AM P99519; 1 female, AM P99520; Coles Bay, 31 December 1964, no collector recorded, 30 males, 42 females and 28 sex uncertain, NMV 54005; Campbelltown, 23 October 1965, no collector recorded, 1 female, NMV J46622; Bruny Island, between Big Lagoon and Little Lagoon, 21 September 1975, R.B. Manning, 3 males, 4 females, NMV J46600; *Victoria*: Elwood Swamp, 18 July 1899, collector unrecorded, 23 males, 24 females, NMV J53989; Elwood, from Sayce collection but no further data but co-types for *E. victoriensis* Sayce, 4 individuals sex uncertain, NMV J68583; Mordialloc, 25 October 1902, collector unrecorded, 1 male, NMV J46622; Cheltenham, 22 October 1910, collector unrecorded, 17 males, 25 females, NMV J53987; Cheltenham, from Sayce collection but no further data, 4 individuals sex uncertain, NMV J54049;

Diagnosis. Egg astroform, projections grooved. First antenna with about 11 lobes, second antenna of about 12 antennomeres. Trunk 18–20 segmented, long palps of claspers with 2–3 palpomeres and palpomere junctions generally inerm. Telson with about 20 dorsal spines, first 3 usually larger and more spaced than others. Cercopod basal section about 60% of total length and bearing about 8 setae of medium length.

Description. *Male: Head* (fig 1b) with ocular tubercle prominent, the compound eye occupying most (~80%) of it. Rostrum slightly more prominent than ocular tubercle, also slightly asymmetrical and with a rounded apex. Ocellus triangular dorsobasially in rostrum. Frons-rostrum angle about 90°. Dorsal organ posterior to eye by about its half its height, pedunculate about height of ocular tubercle.

First antenna (fig. 1b) distinctly longer than peduncle of second antennae, with 11 lobes, each with numerous short sensory setae. *Second antenna* (fig. 1d) with a spinose peduncle subequal to length to the rostrum, each flagellum with 11 antennomeres dorsally with 1–2 spines and ventrally with 1–7 longer setae. Basal and distal antennomeres with minimal spines, setae maximal on antennomeres 4–9 and only 1–3 setae on basal 3 antennomeres.

Carapace (fig. 1a) elongated oval, pellucid and with weakly expressed growth lines, numbering about 9. Older growth lines well spaced compared with closer-spaced newer growth lines near carapace margin. Both anterior and posterior angles hardly noticeable.

Twenty pairs of thoracopods, the first two modified as claspers. Claspers (fig. 1f) with palm (endites IV and V) trapezoidal with a slight rounded protrusion distomedially. Apical club (endite IV) rounded with thick denticles distomedially and many spines apicolaterally, moveable finger (endite VI) of normal curved structure and palps of typical structure. Moveable finger terminating in a suctorial disc and distoventrally with many small pits. Long palp (endite V) subequal in length to the palm in the first clasper and about 1.5× longer in second clasper. Short and long palps, both with three palpomeres with junctions between them inerm. Last palpomere the longest, particularly in the second-longest palp. Other thoracopods of typical structure for *Eulimnadia*, decreasing in size and complexity after 10th thoracopod. Dorsal surface of trunk (fig.1e) with a short spine posteriormedially on each of the 12 posterior trunk segments.

Telson (fig. 1c) with about 20 pairs of dorsal spines, with the first three larger than the next 17, although these generally increase in length posteriorly. Most spines inerm. Caudal

filaments originating from a mound a little higher than the dorsal telsonic floor and between the 4th and 5th spine. This dorsal floor posterior to the mound with a moderate declivity then an even slope to cercopod posterior. Cercopod almost as long as the telson dorsum, the basal 60% hardly thinning to a small naked spine, then rapidly thinning to an acute apex. The basal 60% with about 8 short setae dorsolaterally; length of most about basal cercopod diameter, with setae 5thto 7th longest and the last one the shortest). Many tiny denticles dorsolaterally on apical 40% of cercopod. All setae geniculate. Triangular projection beneath the cercopods at the ventroposterior corner of the telson.

Comments

Three previous authors have commented on aspects of the morphology of this species. Brady's (1886) original description is ambiguous and could apply to many limnadiids. Sayce (1903) notes the 20 trunk segments, which are unusual among *Eulimnadia* and *Paralimnadia* (Timms, 2016a, b), and comments on 20 telsonic spines and proximal half of cercopod bearing about 10 shortish seta Brady's (1886) illustration (Plate XXXII) confirms a rounded protruding rostrum in the male, many growth lines similar to that described presently from the syntypes (Brady, 1886) and a similar clasper also as described presently but with 1–2 spines at the palpomere junctions. Sayce (1903)

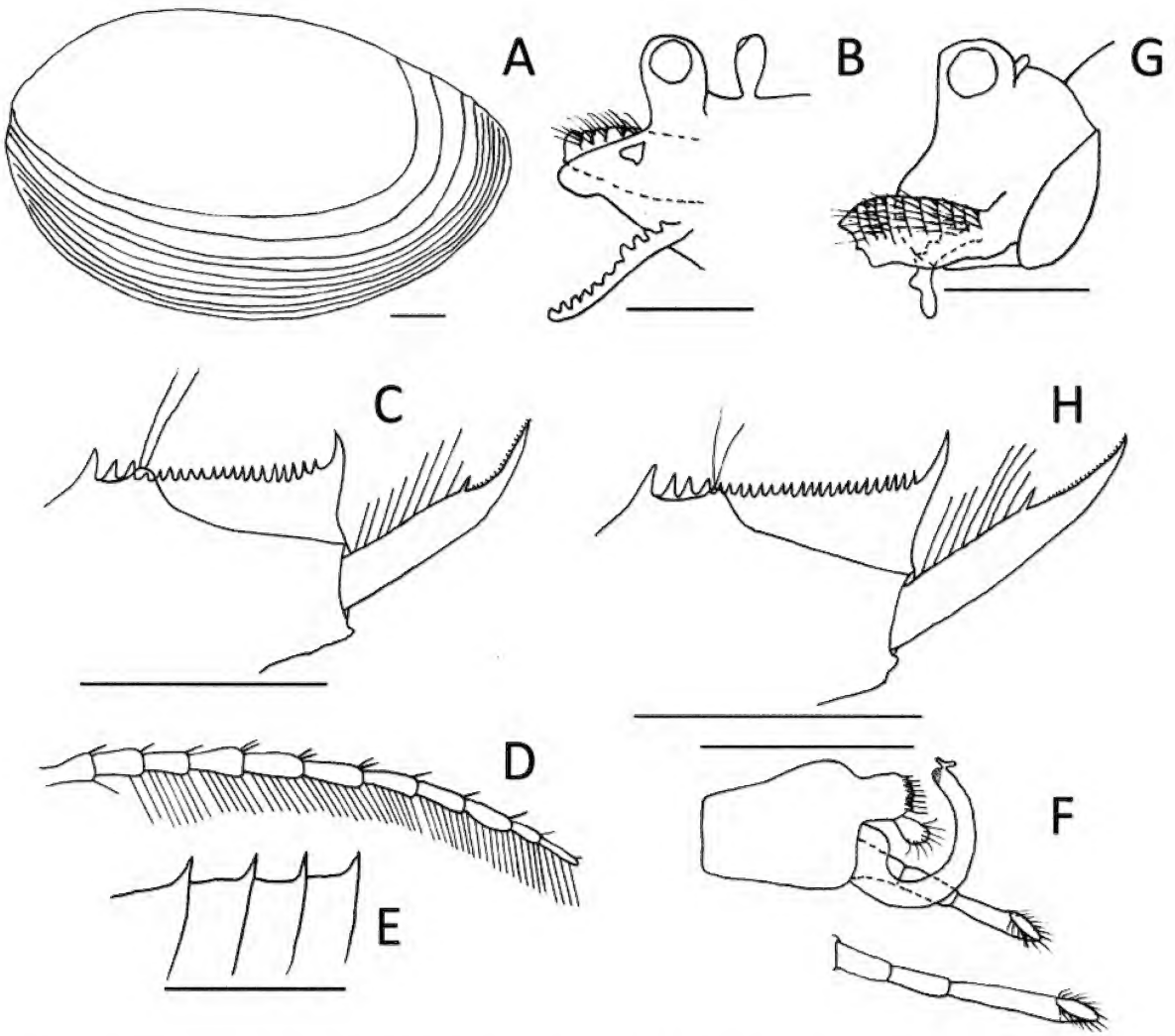

Figure 1. Drawings of types of *P. rivolensis*, male lectotype BMNH 1890.2.1.9. A, carapace; B head, C, telson and cercopod; D, an antennal flagellum; E trunk segments XIV to XVVII dorsa; F, clasper I with insert of long palp of clasper II; female from paralectotype NMV J14426; G, head; H, telson and cercopod. Scale bars 1 mm.

Figure 2. Digital images of male *P. rivolensis* from NMV J55640. A, male carapace; B, male head, C, male telson; D, male claspers, E, female head.

illustrates a third trunk segment with a long palp of endite V, as is typical of *Eulimnadia* and *Paralimnadia* (Timms, 2016a, 2016b). Gurney (1927) illustrates a male telson, which besides showing some variation in size and spacing of 21 telsonic spines, clearly shows a basal cylindrical 45% of the cercopod with 7 setae of moderate length and the telsonic base under the cercopod insertion with a mild triangular protrusion. Gurney (1927) could not find any growth lines. Nowhere in any of these three early descriptions is a subcercopod spine mentioned or illustrated.

This subcercopod spine is also absent in all of the material seen in the Australia Museum and National Museum Victoria, in all cases being replaced by a triangular protrusion of various sizes. Also, given that all specimens examined have 11–12 antennomeres and cercopods with basal 45–60% bearing setae (Timms 2016b), the conclusion is inescapable that this species belongs to *Paralimnadia*, not *Eulimnadia*. Further indication that it is a *Paralimnadia* and not a *Eulimnadia*, although not absolute (Timms, 2016a), is that the sex ratios are

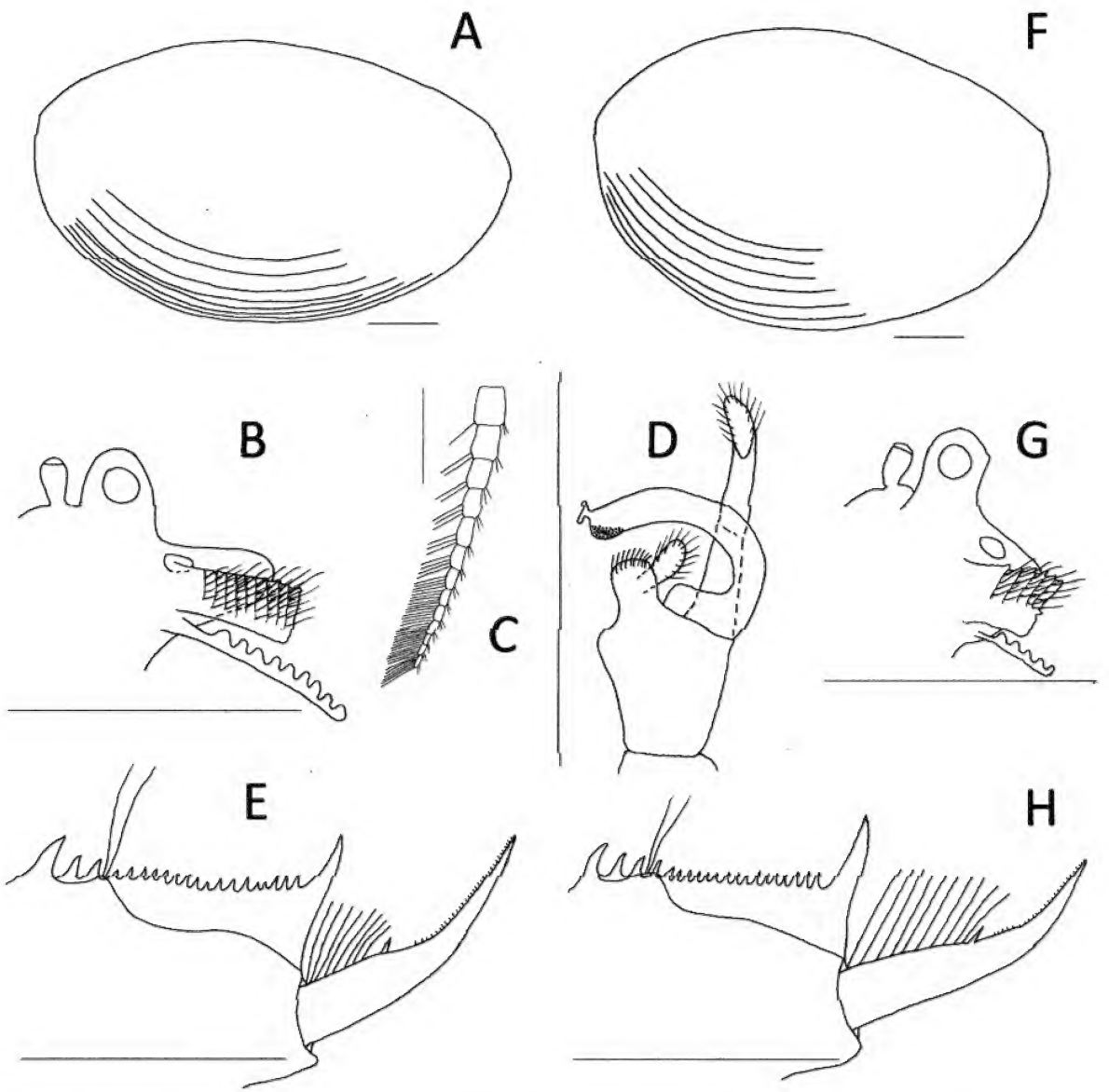

Figure 3. Drawings of male and female of *P. rivolensis* from NMV J55640. A, male carapace; B, male head; C, male antennal flagellum; D, male clasper I, E, male telson; F, female carapace; G, female head; H, female telson. Scale bars 1 mm.

broadly 1:1 and not female or hermaphrodite dominated. This indicates gonochoristic reproduction and not the androdioceous reproduction that is characteristic of *Eulimnadia* (Timms, 2016a, Weeks et al., 2008).

While the lectotype has 20 trunk segments, all other material seen has 18 trunk segments, including the paralectotypes in NMV J14426.

There are no females in among the original syntypes (now lectotype and a paralectotype), so the single female in NMV J14426 was studied (fig. 3).

Head (fig. 3g) with ocular tubercle prominent with a compound eye occupying much of it (50–70% in preserved material). Rostrum a smooth bulge about as prominent as the ocular tubercle and at an angle of about 120° to the frons. Ocellus not visible and dorsal organ apparently missing.

First antenna (fig. 3g) a little shorter than peduncle of the second antenna, and with five small lobes with short sensory setae. *Second antenna* as in male.

Carapace (fig. 3f) as in male, although dorsum more vaulted.

Nineteen *thoracopods* of typical *Eulimnadia* structure. Trunk dorsum with 3–9 setae terminally, these setae few, short and stout on posterior few segments, numerous and longer on segments 8–15, and hardly any setae on anterior trunk segments 1–7.

Telson (fig. 3h) dorsally on each side with 4 larger and more robust spines anteriorly followed by 21 small spines slightly increasing in length posteriorly and terminating in a large spine. Most spines inerm. Telsonic filaments inserted on a mound between the 4th and 5th spines. Cercopod subequal in length to the telson with a cylindrical basal section about 60% of its length followed by a rapidly thinning apical section with many denticles dorsally, the two sections separated by a spine. About 7 setae on the basal section, all a little longer than the diameter of the cercopod, but with the 4th to 6th a little longer again. A blunt triangular projection posteriorly ventral to the cercopod base.

Egg (fig. 4) astroform with 14–20, mean 16.8 ± 2.6 (n = 10) projections, each subtended by 3–8 sharp-edged grooves in different planes arranged radically around its base. One to three of these grooves reach the projection apices on any one aspect of the projection. Projections often bent, length–base ratio varying from 1–2.5 (n = 10). Egg diameter 325 ± 31 μm (n = 10).

Variability. Only the lectotype and paralectotypes have 19–20 trunk segments; all other specimens examined had the usual 18 segments of *Paralimnadia* and *Eulimnadia* (Timms, 2016a,

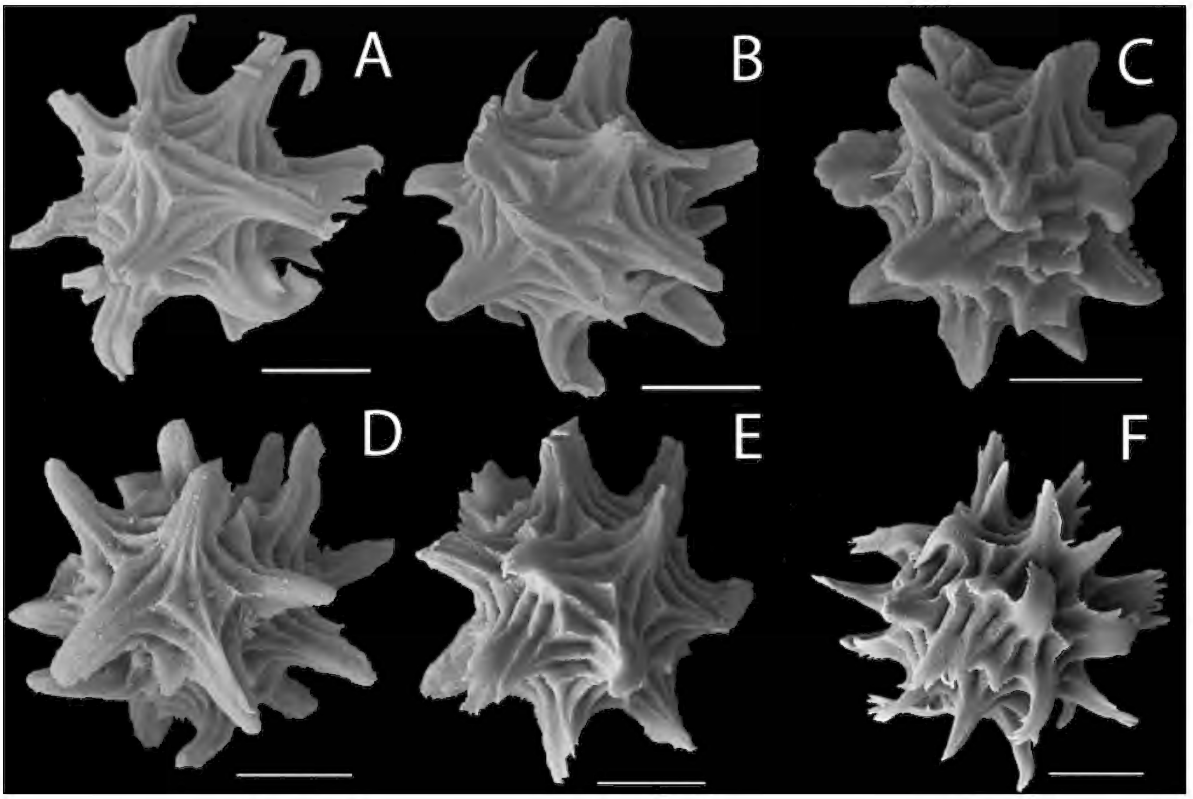

Figure 4. SEM images of eggs of *P. rivolensis*. A, from type locality Rivoli Bay, SA, freshwater swamps, NMV J14426; B, from Campbelltown Tas, AM P55640; C, from Bruny Island, Tas, NMV J46600; D, from Central Australia, NMV J54016; E, from Flinders Island, Tas, AM P97387; F, swamps from near Lake Muir, WA, WAM C57251

2016b). Male antennomeres ranged from 11–13, and lobes on the first antennae perhaps varied by one unit. The number of telsonic spines was more variable (20–26, but typically 21), while the palpomeres and cercopod setae were also variable. Palpomere numbers ranged from 2–3, again the lectotype and paralectotype the only collections with 3 + 3. The cercopod setae ranged from 7–10 and their lengths varied a little from being uniform and of moderate length (i.e. ca. 1.5× cercopod diameter) to being of variable length, some being subequal to cercopod diameter. The lack of a dorsal organ on the female paralectotype is most unusual.

Synonymy of *E. palustera*

This species was originally assigned to *Eulimnadia* on the sole criterion of an apparent spine beneath the cercopod base (Timms, 2015). However, this spine is not a typical subcercopod spine of most *Eulimnadia* but a rather sharp triangular ventroposterior corner of the telson. Hence, an assignment to *Paralimnadia* is necessary. Furthermore, three other features suggest placement in *Paralimnadia*: a cercopod with a spine approximately midlength and not at about 80% of its length, 13 antennomeres rather than about 8, and a sex ratio approximating 1:1, all generally (but not absolutely) indicating *Paralimnadia* (Timms, 2016a, 2016b).

Given the placement of *P. palustera* within *Paralimnadia*, its eggs are identical with those of *P. rivolensis* being astroform with 14–20 projections subtended by 3–8 sharp-edged grooves (fig. 4). Egg morphology has proved to be the most reliable character separating species within *Eulimnadia* (Belk, 1998; Rabet, 2010; Rogers et al., 2012; Timms, 2016a) and *Paralimnadia* (Timms, 2016b). The next most reliable species indicator in both genera is the nature of the cercopod setae. Both *P. palustera* and *P. rivolensis* have about 8 medium length (i.e. 1–2× cercopod diameter) setae (cf. fig. 6 in Timms, 2015 and figs 1–3). Again, both species have about 21 telsonic spines, although spacing is different in the two species. In *P. rivolensis*, all are evenly sized and spaced, except for the first three, which are larger and more spaced. In *P. palustera*, the telsonic spines are mixed in size (cf. fig 6 in Timms 2015 and figs 1–3). Two characters generally of poor differentiating ability are the first antennae and rostrum, although in these two species, there are only minor differences (cf. fig 6 in Timms and figs 1–3).

The claspers are somewhat different between the two species. *P. palustera* has a distinct hamulus medially on the hand (endite IV), while *P. rivolensis* has just a slight swelling there. The palps are variable, with 3 palpomeres in the paralectotype of *P. rivolensis*, but only 2 indistinct ones in most other specimens examined. *P. palustera* generally has 3 palpomeres but may have the second division indistinct or incomplete. Sometimes there are spines at palpomere junction 1–2 in *P. rivolensis*. Similar variability has sometimes been observed in a few other *Paralimnadia* species (Timms 2016b).

Distribution. South-western Western Australia, south-eastern South Australia, southern Victoria and Tasmania. There is a single record from central Australia, which is difficult to accept considering the prominent maritime distribution across southern Australia. It has not been collected in Victoria since 1910, its habitat in the swamps of eastern Port Philip Bay being drained and urbanised in the early 1900s. Widespread drainage in the south-east of South Australia seems to have denied it habitat there. The most recent collection from near the type locality is dated 1975, and my expeditions there in the spring of 2010 and winter of 2016 were unsuccessful. Sites in central Tasmania seem (as of March 2018) also to be drained, so that perhaps it now only occurs in refuges of Flinders Island, Kangaroo Island and south-western Western Australia.

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I thank Michael Geddes for passing on to me two collections of *P. rivolensis* from South Australia; the curators and collection managers of the Australian Museum, British Museum of Natural History, National Museum of Victoria, South Australian Museum, for facilitating of loans of collections, Ron Lovett for digital images and D. Christopher Rogers for discussions and criticism of the manuscript.

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Bathyal and abyssal hydroids (Hydrozoa, Leptothecata) from southeastern Australia

(http://zoobank.org/urn:lsid:zoobank.org:pub:D3BA513B-E7D6-41C5-92E4-E643ACA586E1)

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Abstract Watson, J.E. 2019. Bathyal and abyssal hydroids (Hydrozoa, Leptothecata) from southeastern Australia. *Memoirs of Museum Victoria* 78: 65–72.

A biological survey of the zone extending from Tasmania (40 S) to southern Queensland (25 S) and into the Coral Sea (23 S) was carried out along the south-eastern continental margin of Australia in 2017. Hydroids collected included three known species (*Acryptolaria angulata, Cryptolarella abyssicola* and *Zygophylax concinna*), three new species (*Amphisbetia ramifera, Hebella macroplana* and *Lytocarpia parvispiralis*) and two genera (*Hebella* and *Halecium*) not identified to species. *C. abyssicola* was the predominant species in terms of abundance and geographical range.

Keywords South-eastern Australia; six bathyal to abyssal species; *Cryptolarella abyssicola*.

Introduction

A biological survey of the bathyal to abyssal zone along the south-eastern continental margin of Australia was carried out in 2017 under the auspices of the Commonwealth Scientific Industrial Research Organisation (CSIRO), the Museum of Victoria (MV) and the Queensland Museum (QM). The objective of the survey was to determine the biodiversity of the lower bathyal (to 2500 m) and abyssal (to 4000 m) seafloor habitats off south-eastern Australia and the deep-water ecosystems of seven Commonwealth Marine Reserves. The survey was undertaken by the Australian research vessel RV *Investigator* (Cruise V IN2017-V03) and comprised 60 benthic stations sampled from May to June from Tasmania (40 S) to southern Queensland (25 S) and the Coral Sea (23 S).

Field. Thecate hydroids were recovered from stations sampled by various trawling methods at depths from 1151 m to 4173 m. Preliminary sorting of invertebrate material was undertaken by scientific staff on board the ship. Samples were preserved in bulk in 95% ethanol.

Laboratory. Bulk collections were sorted in more detail at the Queensland Museum and specimens were provided to the author by the Queensland Museum. Representative specimens were first stained in an aqueous solution of lignin pink and were then dehydrated over three days by passing through three increasingly concentrated washes in isopropanol (30%, 60% and 100%) followed by three days of washes in xylene (30%, 60% and 100%) to harden the material. Specimens were then permanently mounted on microslides in Malinol mountant and heated for one week at 40° C to harden the mount.

Family Lafoeidae A. Agassiz, 1865

Acryptolaria angulata (Bale, 1914)

Figure 1 a, b

Cryptolaria angulata Bale, 1914: 166, pl. 35, fig. 1.– Bale, 1915: 251.– Stranks 1993: 7.

Acryptolaria angulata.– Blackburn 1942: 111.– Vervoort and Watson 2003: 41 (synonymy).

Record. QM G337451, microslide. Coll: off Fraser Island, Queensland, 25.3253 S, 154.0683 E to 25.3513 S, 154.076 E, 2350–2342 m, beam trawl, 11/06/2017.

Description. A small infertile colony 30 mm long with remnant hydrorhizal stolons. Stem fascicled, polysiphonic tubes thin, irregularly parallel, of same diameter as stolon.

Hydrothecae given off all around stem, tubular, a sharp outward bend in hydrotheca at junction of abcauline wall with stem; some hydrothecae widening almost imperceptibly to margin. Margin circular, everted, rim minutely outrolled; margin usually with many replications.

Perisarc throughout (preserved material) thin and lax.

Table 1. Measurements (in μm) of ***Acryptolaria angulata***

Distance between hydrothecae	900–1140
Hydrotheca	
length from abcauline bend, incl. replications	800–1020
diameter of margin	264–272

Remarks. The strengthening buttresses reported in *Acryptolaria angulata* by Vervoort and Watson (2003) are actually abcauline intrathecal septa; these do not occur in the present specimen. Septae probably develop to strengthen the hydrotheca in strong water movement, not encountered by specimens in quieter deep-water conditions. The marginal replications of the hydrothecae considerably extends their length.

Distribution. A widespread deep-water species recorded from the Indian Ocean, New Caledonia and rarely, New Zealand. The deepest previous record for the species is 913 m at the Kermadec Ridge.

Cryptolarella abyssicola (Allman, 1888)

Figure 1c–e

Cryptolaria abyssicola Allman, 1888: 40, pl. 18, fig. 2, 2a.

Cryptolarella abyssicola.– Marques et al. 2005: 711, fig. 1, Table 1, (synonymy, discussion).

Records. QM G337422, microslide. Coll: off Freycinet, Tasmania, 41.626 S, 149.5515 E to 41.6892 S 149.5843 E, 4022–4052 m, beam trawl, 18/05/2017. QM G337426, microslide. Coll: off Flinders Island Tasmania, 40.386 S, 148.928 E to 40.383 S 148.951 E, 932–1151 m, beam trawl, 20/05/2017. QM G337427, microslide. Coll: off Flinders Island Tasmania, 40.464 S, 149.3967 E to 40.464 S, 149.4255 E, 4114–4139 m, beam trawl, 20/05/2017. QM G337438, microslide. Coll: off Jervis Bay, New South Wales, 35.333 S, 151.258 E to 35.332 S, 151.214 E, 2650–2636 m, beam trawl, 29/05/2017. QM G337439, microslide. Coll: off Newcastle, New South Wales, 33.435 S, 152.702 E to 33.435 S, 152.665 E, 4280–4173 m, beam trawl, 30/05/2017. QM G337443, microslide. Coll: off central New South Wales coast, 30.099 S, 153.596 E to 30.128 S, 153.571 E, 1257–1194 m, beam trawl, 5/06/2017. QM G337448, microslide. Coll: off Byron Bay, New South Wales, 28.0544 S, 154.083 E to 28.097 S, 154.081 E, 999–1013 m, beam trawl, 9/06/2017. QM G337452, microslide. Coll: Coral Sea, Queensland, 23.587 S, 154.194 E to 23.617 S, 154.1947 E, 1013–1093 m, beam trawl, 13/06/2017. QM G337421, Coll: off Freycinet Tasmania, 41.7305 S, 140.1197 E, to 41.7913 S, 149.1558 E, 2751– 2820 m, beam trawl, 18/05/2017. QM G337431, Coll: Bass Strait, 39.552 S, 149.553 E, to 39.496 S, 149.598 E, 4197–4133 m, beam trawl, 23/05/2017. QM G337435, Coll: off Bermagui, New South Wales, 36.418 S, 150.8 E, 3980 m, beam trawl, 26/05/2017. QM G337440. Coll: off Newcastle, New South Wales, 32.985 S, 152.952 E, to 33.015 S, 152.913 E, 2704–2902 m, beam trawl, 31/05/2017.

Description. Small lax colonies to several centimetres high; some colonies fertile.

Colonies fasciculated basally, ultimate branches monosiphonic. Hydrothecae numerous, tubular, given off from around branches in fasciculated sections, more or less subalternate on monosiphonic branches. Hydrotheca adherent to branch for more than half of length, abcauline wall variably concave, adcauline wall convex, curving smoothly outwards, free wall shorter than adnate wall. Hydrotheca narrowing basally but without floor. Margin circular, not everted, without replications.

Gonothecae large, sausage-shaped, adnate to outer stem tubes, body narrow proximally, becoming tubular, abcauline wall minutely wrinkled, orifice wide, circular, upturned to varying degrees.

Perisarc soft and thin throughout, colour (preserved material) grey.

Table 2. Measurements (in μm) of *Cryptolarella abyssicola*

Hydrotheca	
length	800–1800
width of margin	136–192
Gonotheca	
length	1700–2200
maximum width	320–600
width of orifice	336–464

Remarks. Without a discernible floor, the length of the hydrothecae is highly variable, making it difficult to provide a precise estimate of length.

Cryptolarella abyssicola was first described from *Challenger* Station 160 from a depth of 4755 m south of Australia (42°42 S, 134°10 E) (Allman 1888). In his description Allman commented on the "vast depth" from which the species came, and the height of the colony, about 2 inches (=4.5 cm). *C. abyssicola* has since been recorded world-wide from Sierra Leone, the Azores, Tierra del Fuego, Peru and the Antarctic (Marques et al. 2005) and from abyssal depths under several specific names. The present specimens conform well to the redescription and dimensions of the holotype given by Marques et al. (2005). This survey indicates that *C. abyssicola* is a dominant abyssal species around southern Australia.

Distribution. Australia (type locality), Sierra Leone, Azores, Tierra del Fuego, Peru, Antarctic.

Family Hebellidae Fraser, 1912

Hebella macroplana sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:CC386770-19A6-4ACE-8F5C-91F9963120B8

Figure 1f

Record. QM G337336. Holotype, one microslide. Coll: eastern Bass Strait, Victoria, 39.552 S, 149.553 E to 39.496 S, 149.598 E, 4197–4133 m, beam trawl, 23/05/2017.

Description. Five stolonal hydrothecae creeping on stem of an antipatharian. Colony entangled with remnants of an unidentifiable anthoathecate hydroid.

Hydrorhizal stolon smooth, thin. Pedicel of hydrotheca short, smooth, curved, passing upwards to diaphragm. Hydrothecae tubular, very large, slightly asymmetrical or symmetrical, adcauline side convex to above diaphragm, walls smooth to margin. Diaphragm a barely discernible transverse or slightly oblique ring. Margin circular, slightly everted, one hydrotheca with two widely separated marginal replications.

Perisarc very thin, smooth.

Table 3. Measurements (in μm) of *Hebella macroplana*

Hydrorhizal stolon, width	60–64
Hydrotheca	
length, diaphragm to margin	1740–1920
diameter of margin	520–584
diameter at diaphragm	160–192
length of pedicel	120–184

Remarks. One hydrotheca contains approximately 10 degenerated tentacles indicating that the structure it is not an empty gonotheca. The unsegmented hydrothecal pedicel is very short, and in some hydrothecae it is slightly curved to accommodate the asymmetry of the hydrotheca. The diaphragm varies from a membranous to a thin perisarcal ring.

Three genera considered were *Hebella, Halisiphonia* and *Scandia*; the latter two genera were rejected because they have long hydrothecal pedicels.

Hebella macroplana most resembles the Antarctic species *Hebella plana* Ritchie, 1907; however, the hydrotheca of *H. plana* is much smaller and has a longer and straighter pedicel [see Totton (1930); Briggs (1938); Boero et al. (1997)]. Although the present material is meagre and without gonothecae, the hydrotheca is extremely large and much bigger than any known species.

Etymology. The name alludes to the large hydrotheca compared with that of *H. plana*.

Hebella sp.

Figure 1g

Record. QM G337403, one microslide. Coll: off Bermagui, New South Wales, 36.418 S, 150.8 E, 3980 m, beam trawl, 26/5/2017.

Description. Three damaged stolonal hydrothecae creeping on stem of *Zygophylax concinna*. Stolon fragmented, very thin, tubular. Hydrothecal pedicel long, unsegmented. Hydrotheca long, expanding from a narrow conical base to diaphragm then gradually becoming tubular. Diaphragm a distinct perisarcal ring. Margin circular, rims fragmented.

Perisarc thin and fragile.

Table 4. Measurements (in μm) of *Hebella* sp.

Hydrorhizal stolon width	40
Hydrotheca	
length, diaphragm to margin	1400
diameter at margin (est.)	368
diameter of diaphragm	144
length of pedicel	240–320

Remarks. Although there are no hydrothecae with intact margins, sufficient remains to provide an estimate of marginal diameter. Although morphologically similar to *Hebella ritchiei* Vervoort, 1966 (=*Lafoea tenellula* Ritchie, 1911) from coastal New South Wales, the hydrothecae of the present material are much larger. The material is inadequate to ascribe it to a new species.

Family Zygophylactidae Quelch, 1885

Zygophylax concinna (Ritchie, 1911)

Figure 2 a, b

Zygophylax concinna Ritchie, 1911: 823, pl. 88, figs 3, 4.

Record. QM G337986, one microslide. Coll: off Bermagui, New South Wales, 36.418 S, 150.8 E, 3980 m, beam trawl, 26/5/2017. QM G337446, one microslide. Coll: off Byron Bay, New South Wales, 28.371 S, 154.6487 E to 28.3875 S, 154.617 E, 3825–3754 m, beam trawl, 9/06/2017.

Description. A broken, heavily fascicled and twisted stem originally about 15 mm long and one stem fragment 8 mm long with one undamaged hydrotheca.

Polysiphonic stem tubes parallel, giving off flaccid monosiphonic branches. Branch internodes long, thin, cylindrical, nodes transverse, narrow, a tumescence above and below node; one or two alternate hydrothecae on internode. Hydrotheca about halfway along internode, inserted on an inflated apophysis, distal node of apophysis transverse.

Pedicel of hydrotheca of one long, rarely two or three cylindrical segments expanding distally to diaphragm. Diaphragm a thin perisarcal ring situated high in hydrotheca; walls of hydrotheca above diaphragm more or less cylindrical or expanding a little to margin. Margin circular, transverse to hydrothecal axis, some slightly inclined, rim everted, often with several strong replications.

Perisarc of polysiphonic tubes thick, hydrocladia thinner, hydrothecae fragile, mostly broken.

Table 5. Measurements (in μm) of *Zygophylax concinna*

Internode	
length	700–780
width at node	40–52
adcauline length of apophysis	40–52
Hydrotheca	
pedicel, length to diaphragm	192–240
pedicel, width	100–140
length, diaphragm to margin excl. replications	320–400
diameter of margin	136–176
diameter of diaphragm	64–76

Remarks. Zygophylax concinna was first recorded from a fine sandy bottom at a depth of 100 m off Sydney, New South Wales (Ritchie 1911). Ritchie's small colony (Ritchie 1911, pl. 88, fig. 3) was probably young. The present specimens are probably parts of much larger complexly branched colonies; otherwise the material generally conforms to Ritchie's description of *Z. concinna*.

Distribution. New South Wales, Australia. This is the second record of the species.

Family Haleciidae Hincks, 1868

Halecium sp.

Record. QM G337429, one microslide. Coll: near Flinders Island Tasmania, 39.462 S, 149.276 E to 39.465 S, 149.242 E, 2760–2692 m, beam trawl, 22/05/2017.

Comment. A large lax tangled, fascicled colony with two hydrothecae. Specimen too badly damaged for description.

Family Sertulariidae Lamouroux, 1812

Amphisbetia ramifera sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:0BB245B8-E3F4-421C-928A-CA2C1FB84A30

Figure 2 c, d

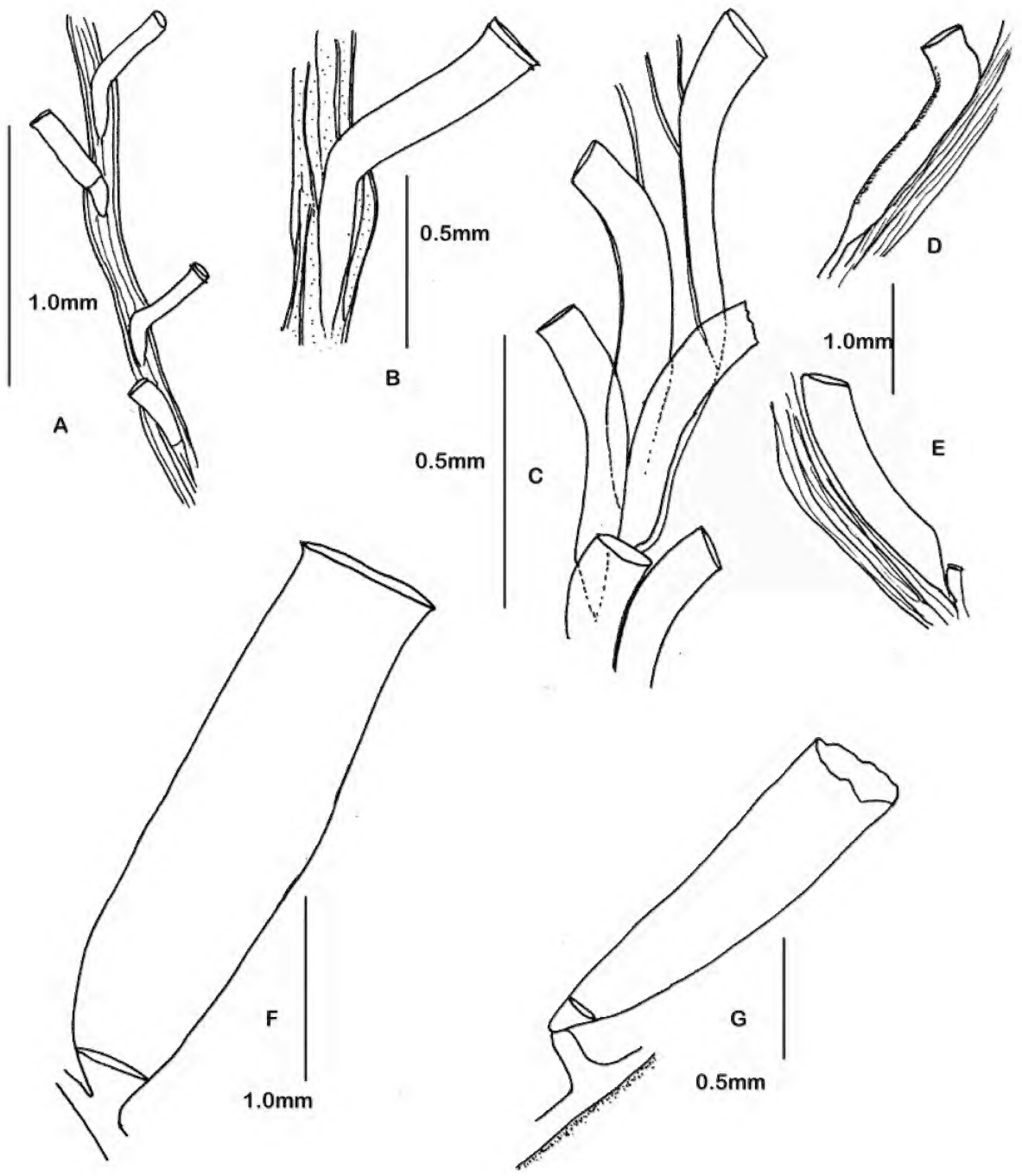

Figure 1. a–g. a, b, *Acryptolaria angulata*. a, distal monosiphonic stem. b, hydrotheca. c–e, *Cryptolarella abyssicola*. c, monosiphonic branch with subalternate hydrothecae. d, gonotheca with wrinkled abcauline wall and upturned margin. e, gonotheca with oblique margin. f, *Hebella macroplana* sp. nov., stolonal hydrotheca. g, *Hebella* sp., stolonal colony and pedicellate hydrotheca.

Record. QM G337425. Holotype, one microslide. Coll: near Flinders Island, eastern Bass Strait, Victoria, 40.386 S, 148.928 E to 40.383 S, 148.951 E, 932–1151 m, beam trawl, 21/05/2017.

Description. A branched stem fragment 5 mm long with four alternate branches on each side; stem and branches monosiphonic. Two tubular subopposite hydrothecae on stem internode, adcauline walls separated, nodes strong, transverse, deeply indented. Apophysis long, narrowing distally to transverse node, an axillar hydrotheca pointing along hydrocladium.

First branch internode long, athecate, expanding slightly to a strong opposed V-shaped joint. Branch internodes same as stem, nodes may be absent but where present transverse to slightly oblique, strongly contracted. Hydrothecae opposite, tubular, base of one hydrotheca usually slightly downwardly displaced with respect to that opposite. Lower adcauline wall of each pair adnate, wall straight to weakly convex basally, the convexity increasing towards free wall; free wall weakly convex or concave to margin. Abcauline wall smoothly concave, some walls slightly bulging just above base. Floor transverse to internode, a small downward septum from adnate wall passing into internode. Margin deep saddle-shaped, flanked by a pair of long, sharp lateral cusps.

Perisarc thick, colour (preserved material) shining golden brown.

Table 6. Measurements (in μm) of *Amphisbetia ramifera*

Stem	
internode length	480–720
width at node	144–200
Branch	
internode length	480–496
width at node	80–108
Hydrotheca	
length of abcauline wall (direct measurement)	176–180
length of adnate adcauline wall (direct measurement)	200–232
length of free adcauline wall	100–112
distance between marginal cusps	116–136
width of floor	112–120

Remarks. The fragment is probably an apical branch of a larger colony. The hydrothecae closely resemble *Amphisbetia minima* (Thompson, 1879), a common shallow water species in Australia and New Zealand. *A. minima* invariably has short unbranched stems unlike the branching habit of *A. ramifera*. In colony size and branching habit, *A. ramifera* resembles *Amphisbetia maplestonei* (Bale, 1884) but in contrast to *A. maplestonei* the hydrocladial hydrothecae of *A. ramifera* are in contact with each other, do not have an abcauline intrathecal septum and the marginal cusps are much more prominent. No other Australian species of *Amphisbetia* has the smoothly outward-curved hydrothecae and such prominent marginal cusps as *A. ramifera*.

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Lytocarpia parvispiralis sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:DD8BF2A6-A3A6-4156-AB1E-1F03B1D2C408

Figure 2 e, f

Record. QM G337453. Holotype, one microslide. Coll: Coral Sea, Queensland, 23.7503 S, 154.5718 E to 23.7739 S, 154.5464 E 2093–2156 m, Brenke epibenthic sled, 14/06/2017. QM G337985. Paratype, one microslide from holotype colony.

Description. Infertile colony 90 mm long, broken in two. Hydrorhiza comprising a group of smooth tubular stolons coalescing to form parallel polysiphonic tubes of lower stem. Colony with three primary branches on upper stem section. Branches monosiphonic, cylindrical, with a row of up to 15 nematothecae below first hydrocladium.

Hydrocladia with many hydrothecae. Hydrocladium long, lax, apophysis large, distal node oblique, two nematothecae in a line below hydrocladium and one beside axil. Hydrocladial internode narrow, node distinct, slightly oblique, two partial septa passing into internode from base of hydrotheca, one below hydranth, the other about halfway along internode.

Hydrotheca occupying much of internode, slipper-shaped, abcauline and adcauline hydrothecal walls gently convex, adcauline wall fully adnate to internode. Margin slightly oblique to internode axis, anterior cusp tongue-shaped, followed by two moderately pointed cusps then three indefinite low cusps, interspaces between very shallow.

Median nematotheca digitate, very short, almost entirely adnate to hydrotheca, terminal orifice small, pointing upwards, open down to hydrotheca. Lateral nematotheca tubular, just reaching margin of hydrotheca, orifice sinusoidal down to internode. Cauline nematothecae the same as laterals. Hydranth with approximately 10 tentacles, hypostome mound-shaped.

Perisarc moderately thick throughout colony.

Table 7. Measurements (in μm) of *Lytocarpia parvispiralis*

Branch	
length of internode	568–648
width at node	144–152
Hydrocladium	
length of internode	608–632
width of node	68–88
Hydrotheca	
depth, posterior to margin (abcauline wall)	320–424
width of margin	208–240
length of median nematotheca	160–168
length of lateral nematotheca	80–112

Remarks. Unfortunately the preserved colony was not examined in detail prior to mounting. Its position on the microslide now prevents determination of whether the hydrocladia were spirally arranged. Its close resemblance to *Lytocarpia spiralis* (Totton, 1930) suggests that the hydrocladia may be spirally arranged. The hydrothecae are much smaller and the marginal cusps less prominent than in *L. spiralis* (see Vervoort and Watson 2003). *Lytocarpia parvispiralis* is clearly an abyssal congener of *L. spiralis,* a species common around New Zealand to depths of 1126 m.

Etymology. The name alludes to the smaller size of *L. parvispiralis* compared to its close congener *L. spiralis*.

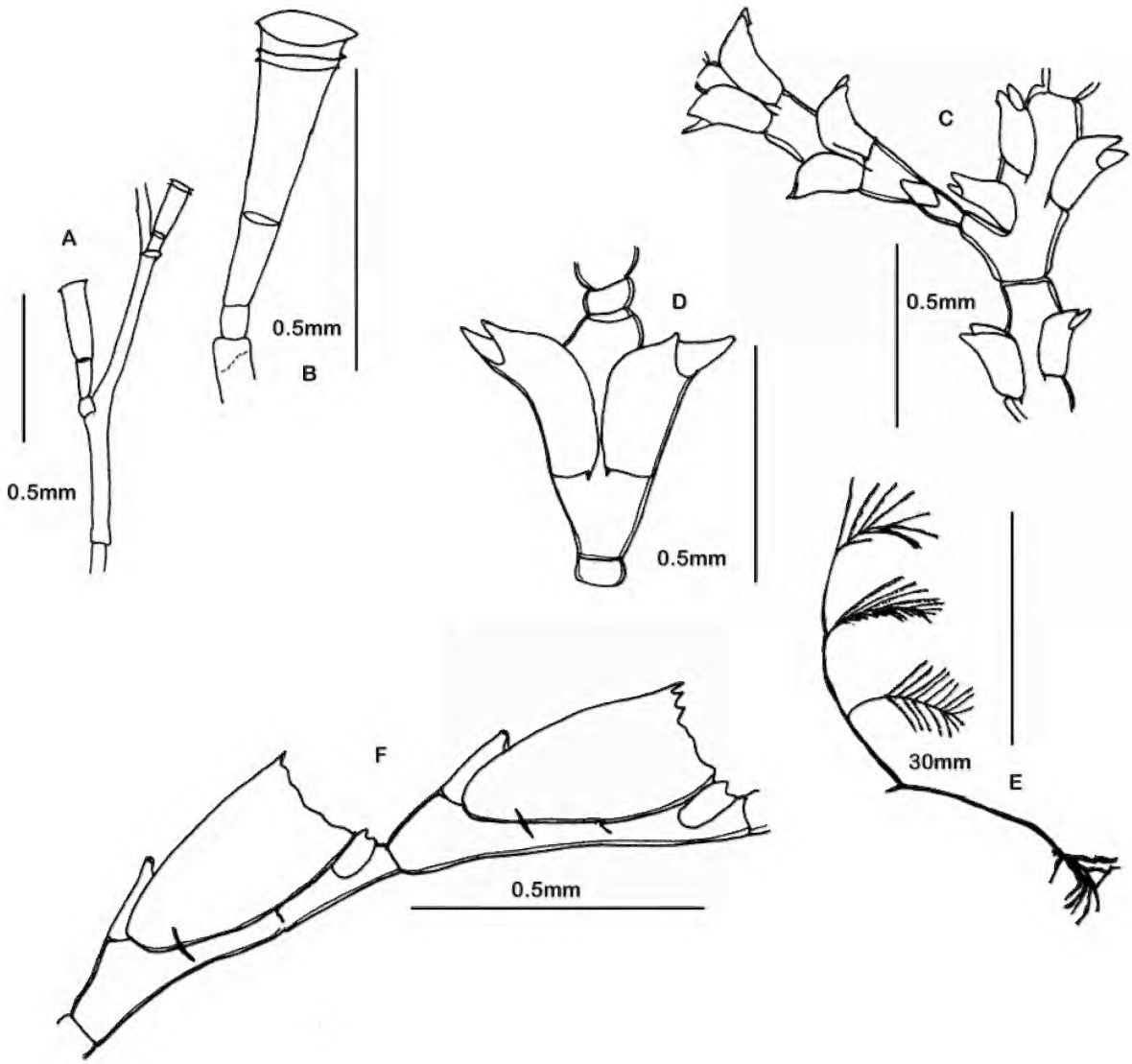

Figure 2. a–f. a, b, *Zygophylax concinna*. a, branch internodes with hydrothecae. b, hydrotheca. c, d, *Amphisbetia ramifera* sp. nov. c, stem with subopposite hydrothecae and axillar hydrotheca. d, branch with opposite hydrothecae. e, f. *Lytocarpia parvispiralis* sp. nov. e, holotype colony. f, hydrothecae, lateral view.

Discussion

Eight species were recovered from depths of 1151–4173 m. Species and their general localities are listed for comparison in Table 8. The list includes three previously known species (*Acryptolaria angulata, Cryptolarella abyssicola* and *Zygophylax concinna*), three newly described species (*Hebella macroplana, Amphisbetia ramifera* and *Lytocarpia parvispiralis*) and two species (*Hebella* sp. and *Halecium* sp.) which were too inadequate or in too poor a condition for identification.

Table 8. Species and their general locations.

Species	Records	General Location
Acryptolaria angulata (Bale, 1914)	1	Off Fraser Island, Queensland
Cryptolarella abyssicola (Allman, 1888)	12	Southern and eastern Australia
Hebella macroplana sp. nov.	1	Eastern Bass Strait, Victoria
Hebella sp.	1	Off Bermagui, New SouthWales
Zygophylax concinna (Ritchie, 1911)	2	Off Bermagui, New SouthWales
Halecium sp.	1	Off Flinders Island, Tasmania
Amphisbetia ramifera sp. nov.	1	Off Flinders Island, Tasmania
Lytocarpia parvispiralis sp. nov.	1	Coral Sea

Abyssal hydroids first recorded from the Australian region were *Cryptolarella abyssicola* and *Halisiphponia megalotheca* from *Challenger* Station 160 from a depth of 4755 m south of Australia (Allman 1888). There are no other published reports of the abyssal hydroid fauna of Australia. Previous moderately deep-water surveys from which hydroids have been reported are from the Great Australian Bight carried out by *F.I.S. Endeavour* (Bale 1914a; 1914b; 1915), the *Thetis* expedition off the coast of New South Wales (Ritchie 1911) and a recent survey of a marine protected area in the eastern Great Australian Bight (Watson 2018). None of these surveys were to depths greater than 100 m.

Cryptolarella abyssicola was by far the most abundant species with 12 records. The species has previously been recorded under various names from Sierra Leone, the Azores, Tierra del Fuego, Peru and the Antarctic (see Marques et al. 2005). It is considered a wide-ranging "true abyssal hydroid" (Vervoort 1985) recorded from 4600 m in the Southern Ocean (Allman 1888), from 2470 m in the Kermadec Trench (Vervoort 1966), from 6328 m from Peru (Vervoort 1972), and 4578 m from the mid-Atlantic Ridge (Calder and Vervoort 1998). The Australian range of *C. abyssicola* is now extended along the south-eastern Australian coast from cool temperate Tasmania in the south to the subtropical Coral Sea in the north.

Acryptolaria angulata is known from deep water in the Indian Ocean, Indo-west Pacific, New Caledonia and New Zealand (Vervoort and Watson 2003). *Zygophylax concinna* has been recorded only once previously from off Sydney (Ritchie 1911); the two new records extend its range south along the New South Wales coast and its depth range from 100 m to 3754 m.

Two newly described species, *Hebella macroplana* and *Amphisbetia ramifera,* were recovered from depths of 4133 m and 4131 m respectively in adjacent localities in eastern Bass Strait, Victoria. The record of *A. ramifera* at such depth is worthy of comment: branched, golden-brown species of *Amphisbetia* are a moderately common component of the shallow coastal water hydroid fauna of southern Australia (Watson 1973; pers. obs.). The present specimen may be a floating fragment from a shallow water colony entrained in the trawl.

The third newly described species, *Lytocarpia parvispiralis* from the Coral Sea, may, when more material is found, prove to be a diminutive subspecies of *Lytocarpia spiralis,* a common deep-water species from around New Zealand (Vervoort and Watson 2003).

There were surprisingly few species and few locality records in the collection considering the extensive latitudinal range of the survey. This may be an artefact of decrease in hydroid diversity with depth, the sampling gear or sampling of predominantly sedimentary substrates.

Acknowledgements

I thank Dr Merrick Ekins of the Queensland Museum and Dr Tim O'Hara of Museum Victoria for the opportunity to examine the hydroid collection. I also thank Josh Hatton of the Queensland Museum for sorting of hydroids and the scientific staff and crew of R.V. *Investigator* for their work during the *Investigator* IN2017-VB03 Cruise.

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A new classification of Callianassidae and related families (Crustacea: Decapoda: Axiidea) derived from a molecular phylogeny with morphological support

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Abstract

Poore, G.C.B., Dworschak, P.C., Robles, R., Mantelatto, F., and Felder, D.L. 2019. A new classification of Callianassidae and related families (Crustacea: Decapoda: Axiidea) derived from a molecular phylogeny with morphological support. *Memoirs of Museum Victoria* 78: 73–146.

The classification of the families and genera of Callianassidae and related families (Crustacea: Decapoda: Axiidea) is significantly revised based on the results of a separately published molecular phylogeny with morphological support. Seven families are recognised: Anacalliacidae Manning and Felder, 1991; Callianassidae Dana, 1852; Callianopsidae Manning and Felder, 1991; Callichiridae Manning and Felder, 1991; Ctenochelidae Manning and Felder, 1991; Eucalliacidae Manning and Felder, 1991; and Paracalliacidae Sakai, 2005.

The families comprise 53 genera, 17 new:

Anacalliacidae—*Anacalliax* de Saint Laurent, 1973.

Callianassidae—*Aqaballianassa* gen. nov.; *Arenallianassa* gen. nov.; *Biffarius* Manning and Felder, 1991; *Callianassa* Leach, 1814; *Caviallianassa* gen. nov.; *Cheramoides* Sakai, 2011; *Cheramus* Bate, 1888; *Coriollianassa* gen. nov.; *Filhollianassa* gen. nov.; *Fragillianassa* gen. nov.; *Gilvossius* Manning and Felder, 1992; *Joculliannassa* gen. nov.; *Lipkecallianassa* Sakai, 2002; *Necallianassa* Heard and Manning, 1998; *Neotrypaea* Manning and Felder, 1991; *Notiax* Manning and Felder, 1991; *Paratrypaea* Komai and Tachikawa, 2008; *Poti* Rodrigues and Manning, 1992; *Praedatrypaea* gen. nov.; *Pugnatrypaea* gen. nov.; *Rayllianassa* Komai and Tachikawa, 2008; *Rudisullianassa* gen. nov.; *Scallasis* Bate, 1888; *Spinicallianassa* gen. nov.; *Tastrypaea* gen. nov. and *Trypaea* Dana, 1852.

Callianopsidae—*Bathycalliax* Sakai and Türkay, 1999; *Callianopsis* de Saint Laurent, 1973; and *Vulcanocalliax* Dworschak and Cunha, 2007.

Callichiridae—*Audacallichirus* gen. nov.; *Balsscallichirus* Sakai, 2011; *Calliapagurops* de Saint Laurent, 1973; *Callichirus* Stimpson, 1866; *Corallianassa* Manning, 1987; *Glypturoides* Sakai, 2011; *Glypturus* Stimpson, 1866; *Grynaminna* Poore, 2000; *Karumballichirus* gen. nov.; *Kraussillichirus* gen. nov.; *Laticallichirus* Komai, Yokooka, Henmi and Itani, 2019; *Lepidophthalmus* Holmes, 1904; *Michaelcallianassa* Sakai, 2002; *Mocallichirus* gen. nov.; *Mucrollichirus* gen. nov.; *Neocallichirus* Sakai, 1988; and *Thailandcallichirus* Sakai, 2011.

Ctenochelidae—*Ctenocheles* Kishinouye, 1926; *Ctenocheloides* Anker, 2010; *Dawsonius* Manning and Felder, 1991; *Kiictenocheloides* Sakai, 2013; *Gourretia* de Saint Laurent, 1973; *Laurentgourretia* Sakai, 2004; and *Paragourretia* Sakai, 2004.

Eucalliacidae—*Andamancalliax* Sakai, 2011; *Calliax* de Saint Laurent, 1973; *Calliaxina* Ngoc-Ho, 2003; *Eucalliax* Manning and Felder, 1991; *Eucalliaxiopsis* Sakai, 2011; *Pseudocalliax* Sakai, 2011; and *Paraglypturus* Türkay and Sakai, 1995.

Paracalliacidae—*Paracalliax* de Saint Laurent, 1979.

Of 19 available family-level names that have accumulated since 1852, ten have been previously synonymised or are synonymised in this work. Of 74 available genus-level names of extant species, 43 have been previously synonymised. The following are synonymised in this work. *Anacalliaopsis* Sakai, 2011, is synonymised with *Anacalliax* de Saint Laurent, 1973. *Nihonotrypaea* Manning and Tamaki, 1998, and *Pseudobiffarius* Heard and Manning, 2000, are synonymised with *Neotrypaea* Manning and Felder, 1991. *Calliaxiopsis* Sakai and Türkay, 2014; *Bakercalliax* Sakai, 2018; *Heardcalliax* Sakai, 2018; and *Manningcalliax* Sakai, 2018, are synoymised with *Eucalliaxiopsis* Sakai, 2011. *Forestcallichirus* Sakai, 2011, and *Capecalliax* Sakai, 2011, are synonymised with *Balsscallichirus* Sakai, 2011. *Podocallichirus* Sakai, 1999; *Lepidophthalmoides* Sakai, 2011; and *Lepidophthalminus* Sakai, 2015, are synonymised with *Lepidophthalmus* Holmes, 1904. *Sergio* Manning and Lemaitre, 1994, and *Callichiropsis* Sakai, 2010, are synonymised with *Neocallichirus* Sakai, 1988. *Ivorygourretia* Sakai, 2017; *Plantesgourretia* Sakai, 2017; and *Ruiyuliugourretia* Sakai, 2017, are synonymised with *Gourretia* de Saint Laurent, 1973. *Heterogourretia* Sakai, 2017, and *Tuerkaygourretia* Sakai, 2017, are synoymised with *Paragourretia* Sakai, 2004.

Keys are presented to families and to genera within families. All available species names are tabulated within the new family and genus arrangement. Some remain *incertae sedis* because they have been only partially described.

Accepted species of Callianassidae and related families number 265, excluding junior synonyms, of which one third (87) are placed in new genus–species combinations. These are tabulated alphabetically by species and in systematic order.

Keywords Crustacea, Decapoda, Axiidea, Anacalliacidae, Callianassidae, Callianopsidae, Callichiridae, Ctenochelidae, Eucalliacidae, Paracalliacidae, taxonomy, new genera

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Introduction

The earliest published descriptions of callianassids were at the end of the 18th century and the beginning of the 19th century (fig. 1). The genus name *Callianassa* Leach, 1814, was introduced shortly thereafter. The number of available species names now totals 305, with 262 accepted by WoRMS (2019) at the time of writing, twice that number if fossils are included. However, despite 72 more generic names having been erected over the last 200 years, authors remain undecided about the generic affinities of new species and *Callianassa* continues to be used as a catch-all genus. The affinities of many species have changed over time, some often, such that about 940 generic recombinations now exist (Sakai, 2011, and later papers), which is more than three times the number of accepted species.

The unsatisfactory state of ghost shrimp systematics has been recently outlined by us in a linked study on which this paper depends (Robles et al., in press). Here, we present a classification of the family and genera of Callianassidae and related families based on Robles et al.'s (in press) phylograms that were derived by multigene analysis of two mitochondrial (16S, 12S) and two nuclear (histone 3, 18S) markers from 123 named species, one half of all extant described species (265 species; WoRMS, 2019), including 24 as yet undescribed or not confidently identified to species. The present phylogeny was supported by a parsimonious analysis of morphological data from 195 species that recovered terminal clades compatible with those of the genetic analyses, though not always with the same deep relationships between terminal taxa. Fitting the morphological data to the molecular phylogram discovered characters that could be viewed as synapomorphies of terminal clades that we treated as families and genera.

As in Robles et al. (in press), we use "callianassoid" as a short-hand term to refer to a monophyletic group of taxa that includes Ctenochelidae and Callianassidae (sensu Dworschak et al., 2012; Poore et al., 2014) in a well-supported clade found in the most recent molecular treatment of "Thalassinidea" (Robles et al., 2009) and subclades Eucalliacinae, Ctenochelidae and Callianassidae (Callichirinae and Callianassinae) in another molecular treatment of Callianassidae and related families (Felder and Robles, 2009). The complex taxonomy of Callianassoidea is explained below.

Here, seven callianassoid families of Axiidea and their genera are diagnosed. For diagnoses of the other families, see Sakai (2011) for Axiidae and Strahlaxiidae, see Poore (2015a) for Callianideidae, and see Poore and Collins (2015) for Micheleidae. A key to all families of Axiidea and keys to all callianassoid genera within the seven families are offered. Tables 1 and 2 list all 265 accepted species, synonyms excepted, alphabetically by species and by family and genus, respectively. One third of all species, 87, are in new combinations. Species authorities are given in these tables and are not repeated for the species mentioned by name in this text.

Methods

Representatives of numerous species were examined in museum collections: University of Louisiana, Lafayette (ULLZ); US National Museum of Natural History, Washington (USNM); Florida Museum of Natural History, Gainsville (UF); Naturhistorisches Museum, Vienna (NHMW); Muséum national d'Histoire naturelle, Paris (MNHN); Senckenberg Museum, Frankfurt (SMF); Zoological Museum, Hamburg (ZMH); Phuket Marine Biological Center, Phuket (PMBC); Museums Victoria, Melbourne (NMV); Northern Territory Museum and Art Gallery, Darwin (NTMAG); Australian Museum, Sydney (AM); and Queensland Museum, Brisbane (QM). The morphological data assembled during examination of the literature and examination of specimens representing about 200 of these species were the basis of the phylogenetic analysis (Robles et al., in press). The same data, stored in a DELTA database (Dallwitz, 2010), were used to generate diagnoses of genera. Another DELTA database was assembled for families of Axiidea. The *Diagnose* facility in the interactive key program Intkey was used to discover a combination of three characters that would differentiate families or genera (in those families with three or more genera). Single characters, or more if necessary, that uniquely diagnose a family or genus are in ***bold italics***. Only the aggregate of these characters was used to diagnose families or genera, fewer than were assembled to build the phylograms. The diagnoses generated by DELTA were edited for sense and additional characters were highlighted if these were felt to more readily diagnose genera.

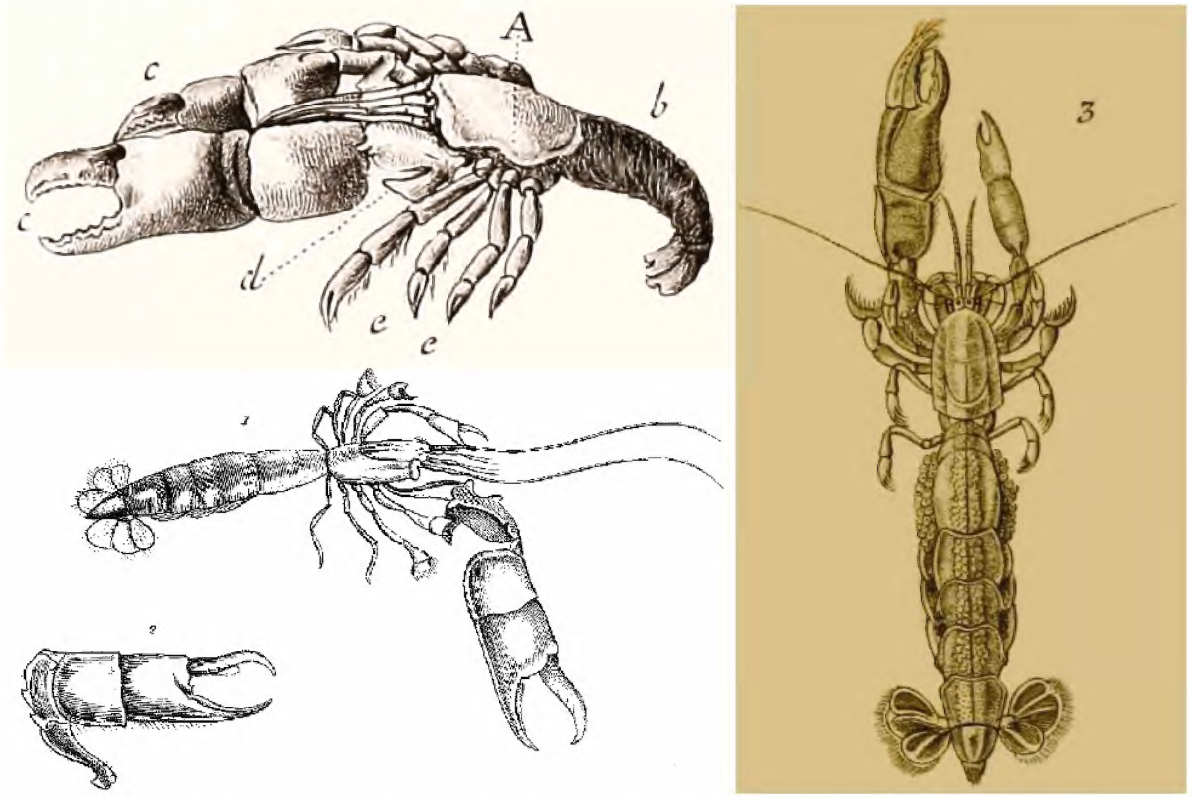

Figure 1. Earliest published figures of callianassids. Clockwise: *Cancer candidus* Olivi, 1792, pl. 3 fig. 3; *Astacus tyrrhenus* Petagna, 1792, pl. 5 fig. 3; *Cancer* (*Astacus*) *subterraneus* Montagu, 1808, pl. 3 figs 1, 2.

To shorten diagnoses, character attributes common to the vast majority of genera in the larger families are not repeated for these genera. These are listed after the keys under the heading *Implicit attributes*, and as a corollary, only the exceptions to these attributes appear in generic diagnoses. For example, a triangular sclerite is absent from the anterior branchiostegite except in *Aqaballianassa*. Intkey was used as an aid to generate dichotomous keys to the families and genera within families, much as explained by Coleman et al. (2010).

Characters used to differentiate families and genera are illustrated by line drawings (figs 2–20) accompanying the keys. Most of these were prepared by tracing published illustrations in Adobe Illustrator but confirmed by our own observations. Illustrations are simplified, rescaled and reoriented for better comparison. The mesial margin of pleopods is on the left. Setae are omitted from these diagnostic drawings unless they are critical characters. Original illustrations, most by GCBP, are identified in figure captions.

Infraorder Axiidea de Saint Laurent, 1979

Axiidea de Saint Laurent, 1979b: 19, 28.—Robles et al., 2009: 310–314.—Dworschak et al., 2012: 187.

Callianassoidea.—Sakai, 2005a: 1125.

Callianassidea.—Sakai and Sawada, 2006: 1357–1358.

Callianassida.—Sakai, 2011: 3.

Remarks. The Axiidea have been diagnosed simply as decapods having pereopods 1 and 2 chelate. The name Axiidea, rather than others suggested by Sakai (2005a, 2011) and Sakai and Sawada (2006), has become almost universally adopted (Poore et al., 2014).

Poore's (1994) Callianassoidea included Laomediidae Borradaile, 1903; Upogebiidae Borradaile, 1903; Callianideidae Kossmann, 1880; Thomassiniidae de Saint Laurent, 1979a; Ctenochelidae Manning and Felder, 1991; and Callianassidae Dana, 1852. This concept was first doubted by a reappraisal of morphology (Sakai, 2005a; Sakai and Sawada, 2006) and later by molecular data (Robles et al., 2009; Tsang et al., 2008). Sakai (2005a) included in Callianassoidea, families Callianassidae; Axiidae Huxley, 1879; Callianideidae; Ctenochelidae and Gourretiidae Sakai,

1999, in fact, all Axiidea. But in a later synthesis, Sakai (2005b) omitted Axiidae and Callianideidae from Callianassoidea. Sakai and Sawada (2006) expanded Callianassoidea to five families. Sakai (2011) included ten families in Callianassoidea, four with two subfamilies each, and included nine families in Axioidea. This dichotomy does not reflect the two clades discovered by investigation of molecular relationships (Robles et al., 2009), where Axiidae are sister to a clade with all other families. This history was summarised by Robles et al. (2009) and Dworschak et al. (2012). The relationships in the phylograms of both Tsang et al. (2008) and Robles et al. (2009) led to our expanded study (Robles et al., in press).

We do not recognise Callianassoidea at the formal superfamily level within Axiidea because, firstly, it has such a convoluted history (outlined above), secondly, doing so leaves other axiidean families hanging, and thirdly, it is impossible to diagnose unambiguously with a unique synapomorphy. Axiidae have been shown to belong to one of two axiidean clades (Robles et al., 2009; Tsang et al., 2008), while the "callianassoid" subclade plus Strahlaxiidae, Micheleidae and Callianideidae belong to the other in a paraphyletic relationship (Robles et al., 2009; Tsang et al., 2008). All callianassoids have a lobster-like form with a flaccid pleon longer than the carapace (but so do most callianideids); all lack a long seta on the triangular posterior lobe of the scaphognathite (but so do some Strahlaxiidae); all have a complete linea thalassinica, a hinge separating the dorsal regions of the carapace from the branchiostegite (but this is partially evident in some Callianideidae); all except one species have flat contiguous eyestalks (but so do callianideids). Pleopods 3–5 of callianassoids have triangular or subtriangular endopods with straight mesial margins that are closely connected to their pairs by short or moderately long appendices internae and exopods that are usually longer than and enclosing the endopods. This condition is less pronounced in some ctenochelids and callianopsids, which approach axiids, strahlaxiids and micheleids in having the endopods of pleopods 3–5 linear or oval, weakly connected to their pairs by long appendices internae, and the exopods shorter than or as long as the endopods, but not enclosing the endopods. Species of *Callianidea* have pleopods 3–5 as in most callianassoids. The uropodal exopod of most callianassoids has an elevated dorsal plate, a region at the end of the anterior margin defined by a transverse row of setae but, again, it is not true of all because a dorsal plate is absent in Callianopsidae, Ctenochelidae and *Paracalliax*.

The number of well-defined clades with consistent molecular support prompted us to recognise seven "callianassoid" families. All had been previously recognised at least as subfamilies. Four other families of Axiidea are Axiidae, Callianideidae, Micheleidae and Strahlaxiidae. The following family diagnoses use 21 characters adequate to distinguish all 11 families. The bold italic parts in diagnoses are character states, generated with the aid of Intkey (Dallwitz, 2010), that distinguish each family from every other family in at least one respect.

Key to families of Axiidea

Figures 2–4

1. Rostrum prominent, often with erect lateral spines, carapace with lateral gastric carinae originating from lateral margins of rostrum, often with submedian and median gastric carinae (figs 2a, b, c); linea thalassinica absent (figs 2e–g); eyestalks cylindrical (figs 2a, b, c) 2

– Rostrum triangular-flat or reduced to short spine shorter than eyestalk, carapace without median and lateral gastric carinae (fig. 2f), *or* rostrum flat-unornamented, longer than eyestalk, carapace with lateral gastric carinae (fig. 2e); linea thalassinica present over all or part of carapace length (figs 2h–o), *or* absent, *or* short; eyestalks contiguous, flat or cylindrical (figs 2d, f, g) 3

2. Rostrum apex bifid, with lateral teeth (fig. 2c); propodi of pereopods 3 and 4 without lateral spiniform setae (fig. 3q); pleopods 3–5 with oblique peduncles meeting mesially, endopods oval, exopods attached laterally, triangular, shorter than endopods, wider proximally than distally (fig. 4p); maxilla scaphognathite with (fig. 3a) or without (fig. 3b) long setae extending from posterior lobe into branchial chamber ..... Strahlaxiidae

– Rostrum with acute or rounded apex (figs 2a, b); propodi of pereopods 3 and 4 with lateral spiniform setae (fig. 3p); pleopods 3–5 with linear peduncles not meeting mesially, endopods linear to elongate-oval, exopods linear-oval, attached subdistally, shorter than or as long as endopod, not overlapping endopods (fig. 4o); maxilla scaphognathite with long setae extending from posterior lobe into branchial chamber (fig. 3a) ..... Axiidae

3. Maxilla scaphognathite with long setae extending from posterior lobe into branchial chamber (fig. 3a); linea thalassinica complete, partial or absent 4

– Maxilla scaphognathite without long setae extending from posterior lobe into branchial chamber (fig. 3b); linea thalassinica complete over full carapace length (fig. 2h) 5

4. Posterior margin of carapace evenly curved, not interacting with anterolateral lobes on pleomere 1 (fig. 2f); eyestalk flat, contiguous (fig. 2f); chelipeds flattened, asymmetrical (fig. 3j) ..... Callianideidae

– Posterior margin of carapace with lateral lobes interacting with anterolateral lobes on pleomere 1 (fig. 2g); eyestalks cylindrical even if continuous (fig. 2g); chelipeds cylindrical, symmetrical (fig. 3i) ..... Micheleidae

5. Pleomere 1 with dorsal pair of lobes interacting with posterior margin of carapace (fig. 2i); female pleopod 1 with single broad expanded ramus (fig. 4b); pleopod 2 (at least of female) similar to pleopods 3–5 (fig. 4c); epipods present above maxilliped 3 to pereopod 4 ..... Paracalliacidae (1 species, *Paracalliax bollorei* de Saint Laurent, 1979)

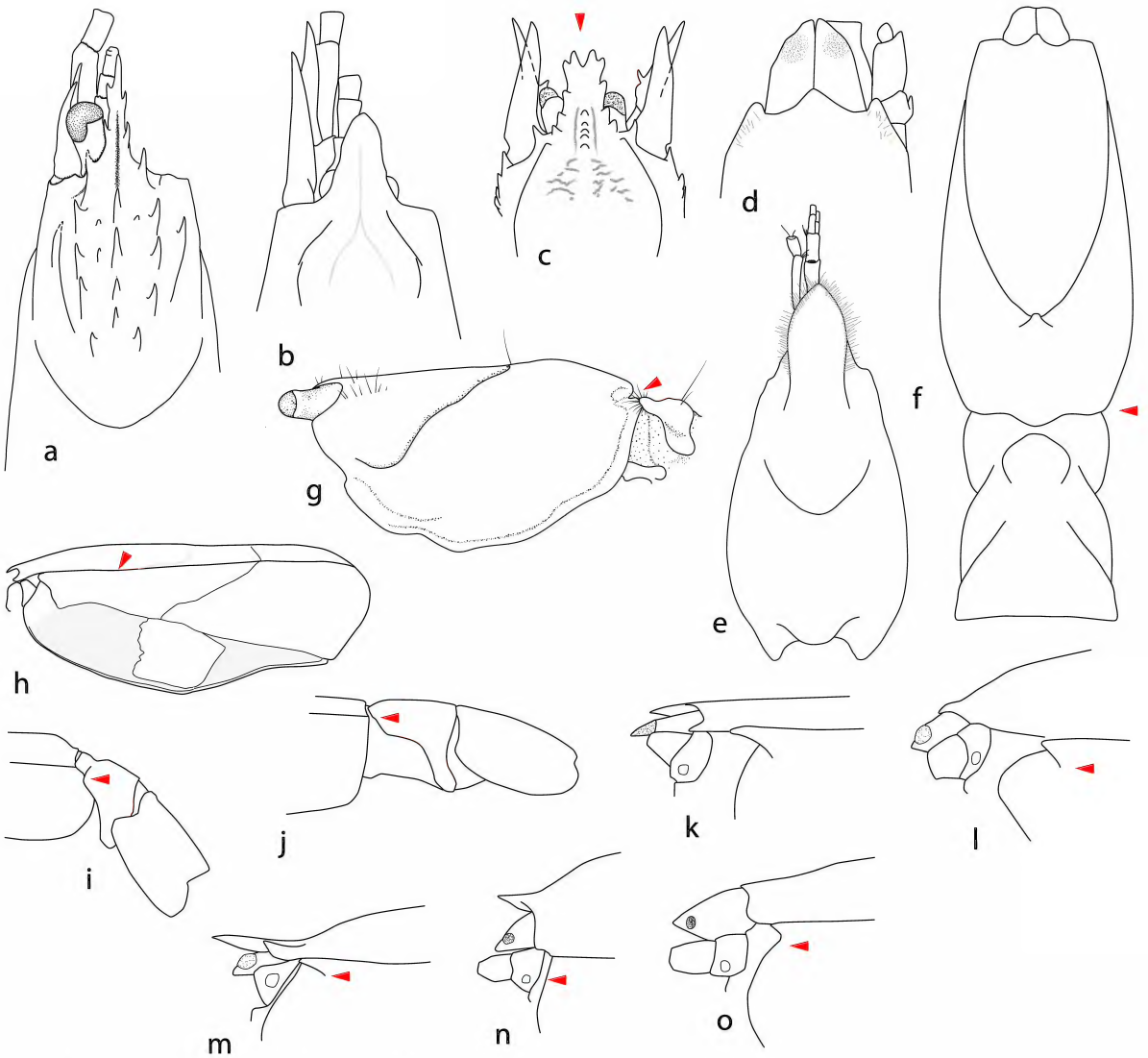

Figure 2. Diagnostic characters for families of Axiidea. Anterior carapace, dorsal: a, Axiidae, *Pillsburyaxius*; b, Axiidae, *Eiconaxius*; c, Strahlaxiidae, *Neaxius*; d, Eucalliacidae, *Calliaxina*; e, Micheleidae, *Tethisea*; f, Callianeidae, *Callianidea*. Carapace, lateral: g, Micheleidae, *Michelea*; h, Eucalliacidae, *Calliaxina*. Posterior carapace, pleomeres 1, 2: i, Paracalliacidae; j, Callianassidae. Anterior carapace, branchiostegite, epistome, basal antenna and eyestalk: k, Eucalliacidae, *Calliaxina*; l, Callichiridae, *Callichirus*; m, Callichiridae, *Lepidophthalmus*; n, Callianassidae, *Coriollianassa*; o, Callianassidae, *Biffarius*.

Original illustrations: i, *Paracalliax bollorei*, MNHN Th1517; k, *Calliaxina sakaii*, ULLZ; l, *Callichirus islagrande*, ULLZ; m, *Lepidophthalmus richardi*, ULLZ; n, *Coriollianassa coriolisae*, MNHN-IU-2014-18276; o, *Biffarius biformis*.

– Pleomere 1 with evenly curved dorsal margin, not interacting with posterior margin of carapace (fig. 2j); female pleopod 1 with reduced ramus (fig. 4a); pleopod 2 in both sexes (figs 5d–g) smaller than pleopods 3–5 (fig. 5q); epipods absent above maxilliped 3 to pereopod 4 (exception, 2 species of Callianopsidae) 6

6. Maxilliped 3 dactylus ovate, distally truncate, with dense distal field of setae (fig. 3e) 7

– Maxilliped 3 dactylus linear, with scattered groups of setae (fig. 3f), *or* densely setose on upper or lower margin (figs 3g, h) 8

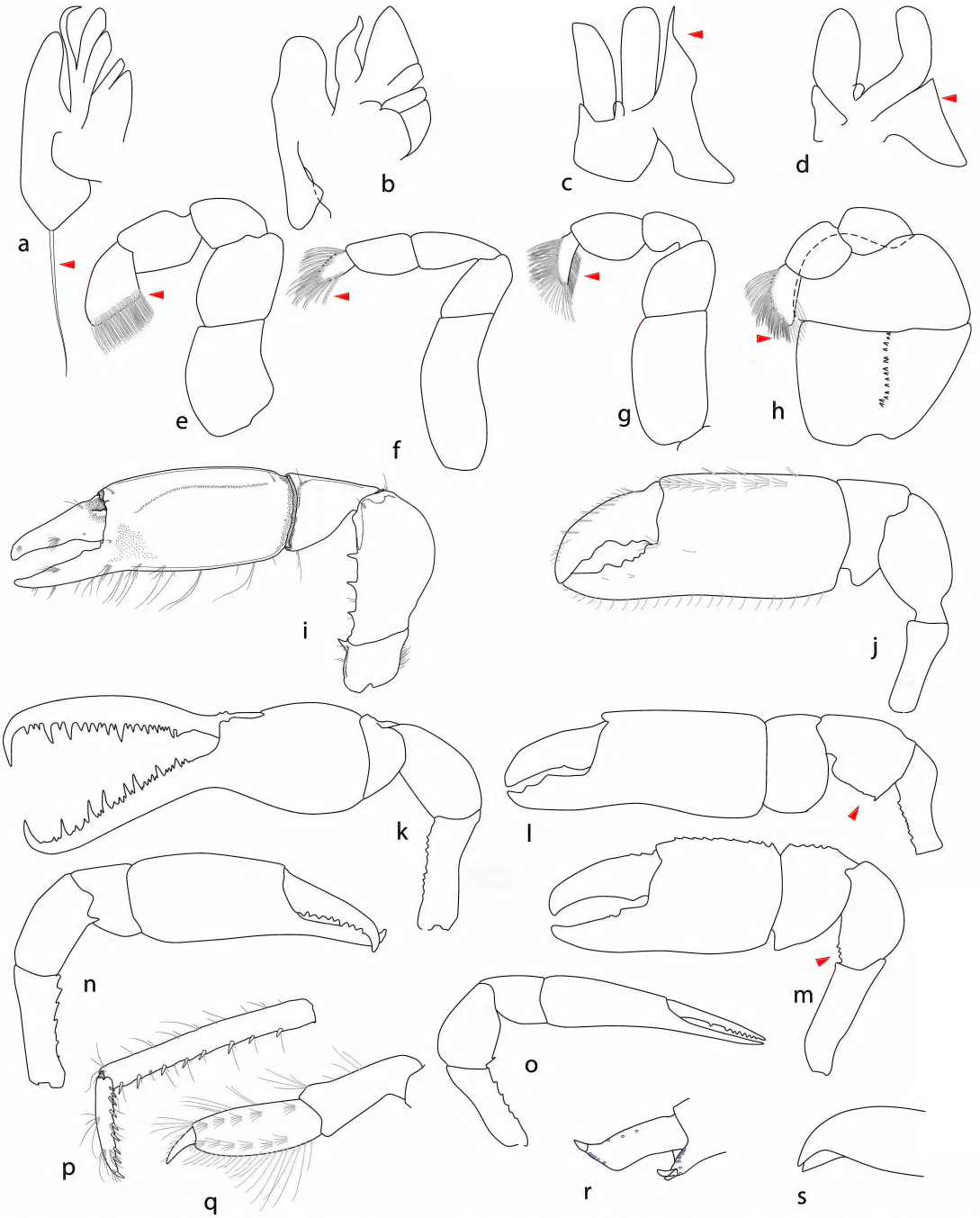

Figure 3. Diagnostic characters for families of Axiidea. Maxilla: a, Axiidae, *Eutrichocheles*; b, Callianassidae, *Arenallianassa*. Maxilliped 1: c, Callichiridae; d, Callianassidae. Maxilliped 3: e, Callianopsidae; f, Anacalliacidae; g, Callianassidae, *Callianassa*; h, Callianassidae, *Caviallianassa*. Major cheliped: i, Micheleidae, *Tethisea*; j, Callianideidae, *Callianidea*; k, Ctenochelidae, *Ctenocheles*; l, Ctenochelidae, *Gourretia*; m, Anacalliacidae. Minor cheliped: n, Ctenochelidae, *Ctenocheles*; o, Ctenochelidae, *Gourretia*. Pereopod 3, propodus, dactylus: p, Axiidae, *Acanthaxius*; q, Strahlaxiidae, *Neaxius*. Pereopod 5, fingers: r, Ctenochelidae, *Ctenocheloides*; s, Anacalliacidae. The arrows indicate features of interest.

Original illustrations: d, *Callianassa subterranea*, NMV J16779; h, *Caviallianassa* FP-11, UF 29204.

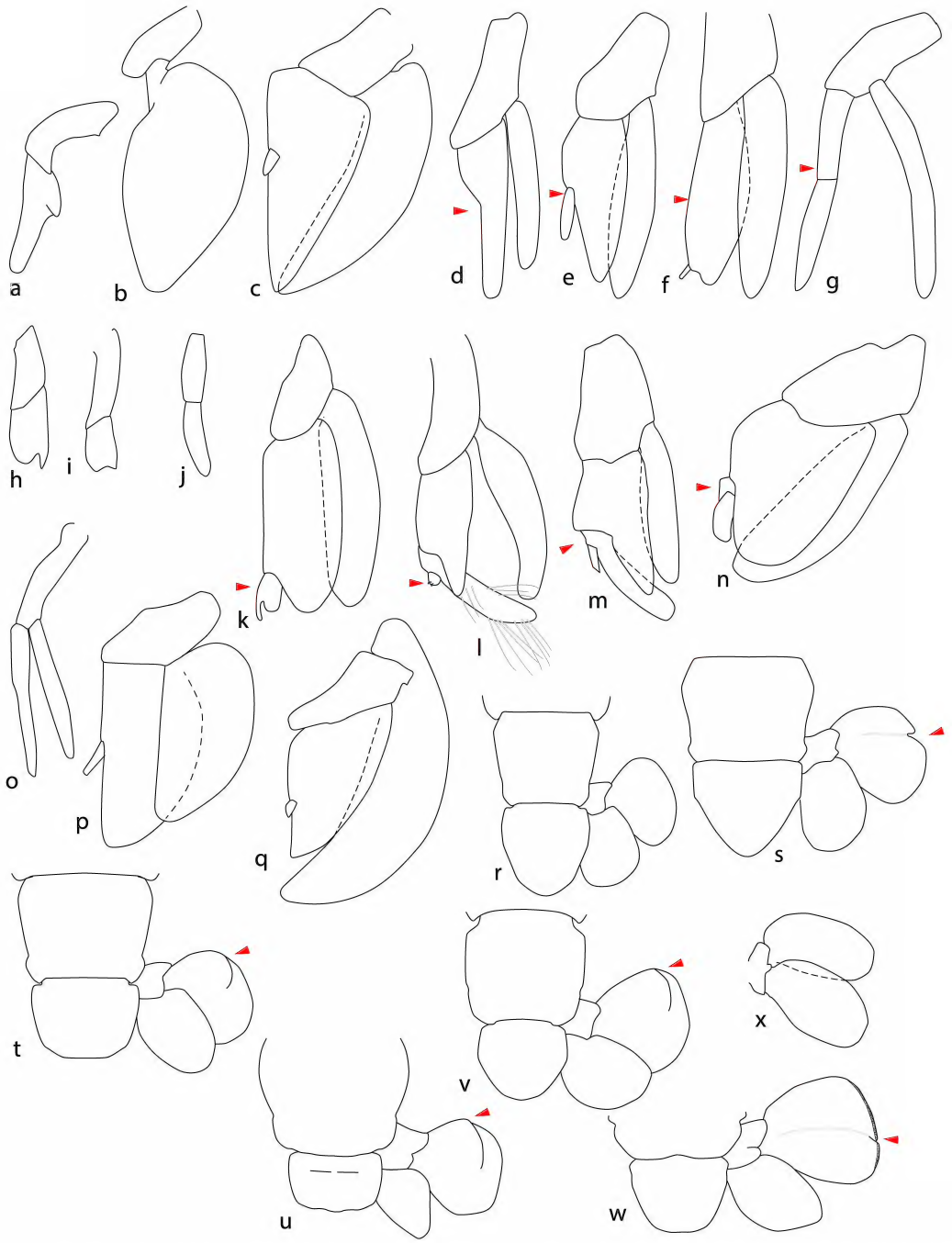

Figure 4. Diagnostic characters for families of Axiidea. Female pleopod 1: a, Eucalliacidae, *Paraglypturus*; b, Paracalliacidae. Female pleopod 2: c, Paracalliacidae; d, Eucalliacidae, *Calliax*; e, Eucalliacidae, *Calliaxina*; f, Callichiridae; g, Callianassidae. Male pleopod 1: h, i, Callichiridae; j, Callianassidae. Male pleopod 2: k, Ctenochelidae, *Ctenocheles*; l, Eucalliacidae, *Eucalliax*; m, Eucalliacidae, *Calliaxina*; n, Eucalliacidae, *Paraglypturus*. Pleopod 3: o, Axiidae, *Marianaxius*; p, Strahlaxiidae, *Neaxiopsis*; q, Callichiridae. Pleomere 6, uropod, telson: r, Ctenochelidae, *Gourretia*; s, Ctenochelidae, *Paragourretia*; t, Eucalliacidae, *Calliaxina*; u, Eucalliacidae, *Eucalliax*; v, Callianassidae; w, Anacalliacidae; x, Callianopsidae. Arrows indicate features of interest.

Original illustrations: s, *Eucalliax quadracuta*, NHMW 25916; w, *Anacalliax agassizi* MNHN Th1206.

7. Uropodal exopod oval, without dorsal plate (fig. 4x); telson parallel-sided over proximal half, then tapering to evenly rounded apex, *or* widest basally over anterior third, sharp lateral step, then tapering posteriorly to broadly rounded apex; maxilliped 3 propodus longer than wide, not prominently lobed on lower margin (fig. 3e); male pleopod 1 with article 2 triangular, with lobed mesial margin, *or* flagellate ..... Callianopsidae

– Uropodal exopod with dorsal plate, indicated by secondary row of setae diverging on upper surface from anterior margin (figs 4t, u); telson convex-sided, widest near midpoint, *or* semicircular, *or* curving to broad convex apex (figs 4t, u); maxilliped 3 propodus about as wide as long; male pleopod 1 with article 2 linear, *or* blade like, with bifid or simple apex, *or* digitiform (sometimes fused) ..... Eucalliacidae

8. Uropodal exopod without dorsal plate (fig. 4r), *or* with distal margin interrupted by weak notch (fig. 4s) 9

– Uropodal exopod with dorsal plate, secondary row of setae on upper surface branching subdistally from anterior margin (fig. 4v) 10

9. Pereopod 5 semichelate (fixed finger closing on proximal part of dactylus), dactylus a twisted plate longer than fixed finger (fig. 3r); major cheliped merus lower margin with weakly toothed squarish blade plus proximal erect spine (fig. 3l), *or* simple proximal spine, *or* oblique blade or spine near midpoint; propodus evenly tapering or cylindrical, with fingers tapering and irregularly toothed or thin and pectinate (fig. 3k); minor cheliped merus with spine on lower margin (figs 3n, o); telson mostly parallel-sided, with rounded posterolateral corners (fig. 4r), *or* parallel-sided over proximal half, then tapering to evenly rounded apex (fig. 4s) ..... Ctenochelidae

– Pereopod 5 chelate (fixed finger closing complete length of dactylus; fig. 3s); major cheliped merus lower margin with 1 or 2 small proximal teeth, propodus parallel-sided, fixed finger as long as dactylus (fig. 3m); minor cheliped merus lower margin smooth; uropodal endopod with small distal notch (fig. 4w); maxilliped 3 ischium linear, with curved lower margin, palp narrow, dactylus linear, generally setose (fig. 3f); telson tapering from greatest width near base (fig. 4w) ..... Anacalliacidae

10. Anterior branchiostegal lobe well-produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle (figs 2l, m); male pleopod 1 article 2 usually of 2 articles, article 2 simple or apically notched (figs 4h, i); male and female pleopod 2 rami narrower and with less setation than pleopods 3–5, endopod flattened and 2–5 times as long as wide (fig. 4f); maxilliped 1 epipod with acute anterior lobe lying obliquely and along oblique suture of exopod (fig. 3c) ..... Callichiridae

– Anterior branchiostegal lobe merging smoothly with anterodorsal branchiostegal angle (figs 2n, o), *or* with small independent triangular sclerite; male pleopod 1 absent, *or* if present, uniarticulate or with second simple article (fig. 4j); male pleopod 2 absent or reduced; female pleopod 2 rami styliform, endopod much longer than wide (fig. 4g); maxilliped 1 epipod truncate, without anterior lobe (fig. 3d) ..... Callianassidae

Anacalliacidae Manning and Felder, 1991

Figure 5

Anacalliinae Manning and Felder, 1991: 786.
Anacalliacinae.—Sakai, 1999a: 126.—Sakai, 2005b: 208–210.
Anacalliacidae.—Sakai, 2011: 341.

Type genus. Anacalliax de Saint Laurent, 1973.

Diagnosis. ***Rostrum flat, short, triangular, shorter than eyestalks***; median carina on rostrum only; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica horizontal in lateral view; anterior branchiostegal margin sinusoidal or semicircular; anterior branchiostegal lobe simple, scarcely calcified, merging smoothly with anterodorsal branchiostegal angle and anterolateral margin of carapace; posterior margin of carapace without lateral lobes, pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite elongate. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. Maxilliped 3 propodus longer than wide, not prominently lobed on lower margin; dactylus slender, digitiform, with setae irregularly spaced along all margins. Cheliped merus lower margin spinose; major cheliped palm oval in cross-section, barely crested above or below. Pereopod 3 propodus broad, with proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate or subchelate. Female pleopod 2 rami narrower and with more reduced setation than pleopods 3–5; endopod 2–5 times as long as wide. Pleopods 3–5 with oblique peduncles, endopods oval, exopods attached laterally, not proximally lobed, shorter than and barely overlapping endopods; appendices internae reduced and almost embedded in mesial margin of endopod. ***Uropodal exopod with margin divided by notch***.

Remarks. The only genus, *Anacalliax* de Saint Laurent, 1973, is recognised by the unique combination of a short flat rostrum and the uropodal exopod having a marginal notch.

The subfamily Anacalliacinae (misspelled Anacalliinae) was erected by Manning and Felder (1991) as one of three subfamilies of Ctenochelidae, the others being Ctenochelinae and Callianopsinae. Manning and Felder (1991) included *Paracalliax*, *Gourretia* and *Dawsonius* in the nominate subfamily and only their type genus in the other two. This arrangement reflects in a single family, with all four basally derived families recognised in Robles et al.'s (in press) analysis as a paraphyletic grouping. Sakai (2005b) treated the taxon as a subfamily of Callianassidae while retaining Gourretiidae for

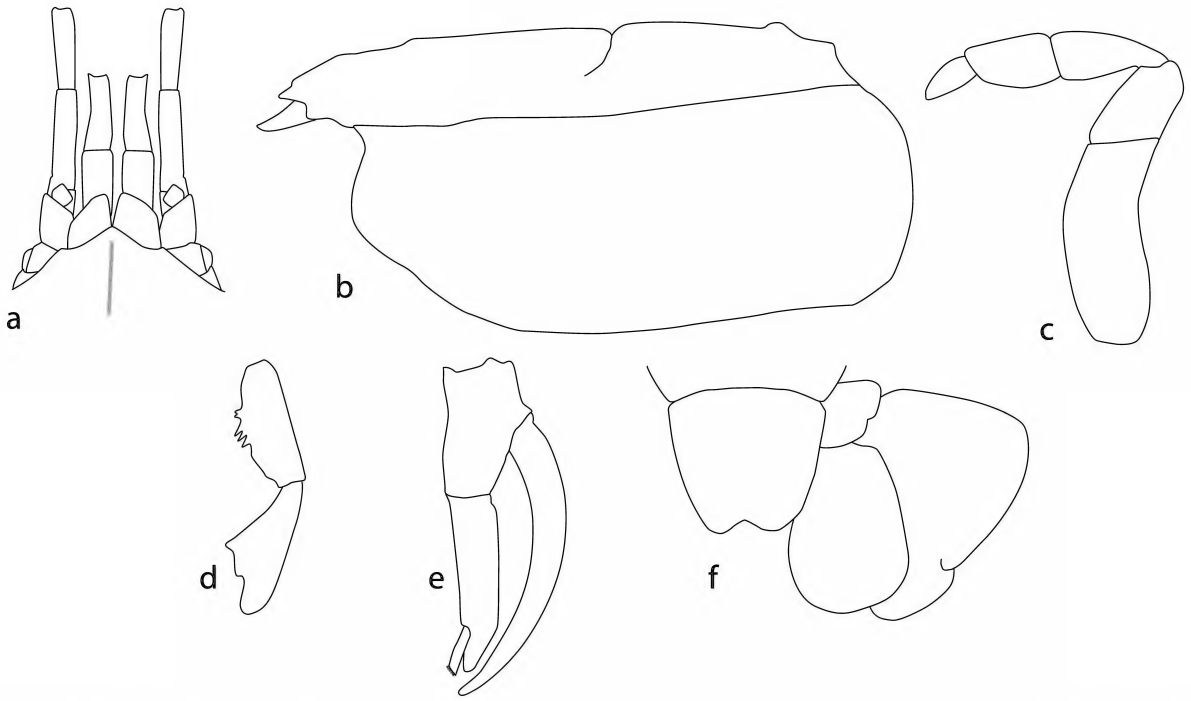

Figure 5. Diagnostic characters of Anacalliacidae, *Anacalliax*: a, dorsal anterior carapace, eyestalks, antennules, antennae; b, lateral carapace; c, maxilliped 3; d, male pleopod 1; e, female pleopod 2; f, telson, uropod.

other subfamilies. Sakai (2011) elevated the taxon to family level. The family comprises a single genus. Two genera erected by Sakai (2011) are herein synonymised, *Anacalliaopsis* with *Anacalliax*, and *Capecalliax* with *Balsscallichirus* (Callichiridae; see below).

The similarity of the "dorsal oval" to that of *Callianassa* s.s. was highlighted in Sakai's (2011) discussion of this group, but this character grades to such an extent throughout all families that we were unable to use it at any level. The broad (almost axiid-like) article 2 of the male pleopod 1, presence of an appendix masculina on the male pleopod 2, absence of any tooth on the merus of the cheliped, absence of a dorsal plate on the uropodal exopod and absence of a distal lobe on the epipod of maxilliped 1 suggest a basal position for this family, as realised by Manning and Felder (1991).

The family is known only from the type material of its two species. No specimen was available for inclusion in the molecular analysis.

Anacalliax de Saint Laurent, 1973

Anacalliax de Saint Laurent, 1973: 515.—Manning and Felder, 1991: 786–787.—Sakai, 1999a: 126.—Sakai, 2005b: 210.—Sakai, 2011: 343.

Anacalliaopsis Sakai, 2011: 342 (type species: *Callianassa agassizi* Biffar, 1971, by original designation and monotypy) **syn. nov.**

Type species. *Callianassa argentinensis* Biffar, 1971b, by original designation and monotypy.

Diagnosis. With characters of the family.

Remarks. The genus is the sole member of the family. Sakai (2011) erected a new genus *Anacalliaopsis* for a single species *Callianassa agassizi*. He did not explain how the species differed from *Anacalliax argentinensis* except in his key where the only difference was in the posterior margin of the telson (other characters used are identical or not compared). *Anacalliax argentinensis* has a concave margin whereas *A. agassizi* has a convex margin, differences that, if substantiated, would be best treated at species level. Otherwise, the two share similar maxillipeds, chelipeds and pleopods.

Callianassidae Dana, 1852

Figures 6–11

Callianassidae Dana, 1852a: 12, 14.—Dana, 1852b: 508.—Bouvier, 1940: 100.—Balss, 1957: 1581.—de Saint Laurent, 1973: 513.—de Saint Laurent, 1979a: 1395.—Manning and Felder, 1991: 766.—Poore, 1994: 101—Sakai, 1999a: 7.—Sakai, 2005b: 9–11.—Sakai and Sawada, 2006: 1357.—Sakai, 2011: 353–357 partim.

Callianassinae.—Bouvier, 1940: 100.—Balss, 1957: 1582.—de Saint Laurent, 1973: 514.—de Saint Laurent, 1979a: 1395–1396.—Manning and Felder, 1991: 767.—Sakai, 1999a: 10.—Sakai, 2005b: 11–25.—Sakai, 2011: 357–358.

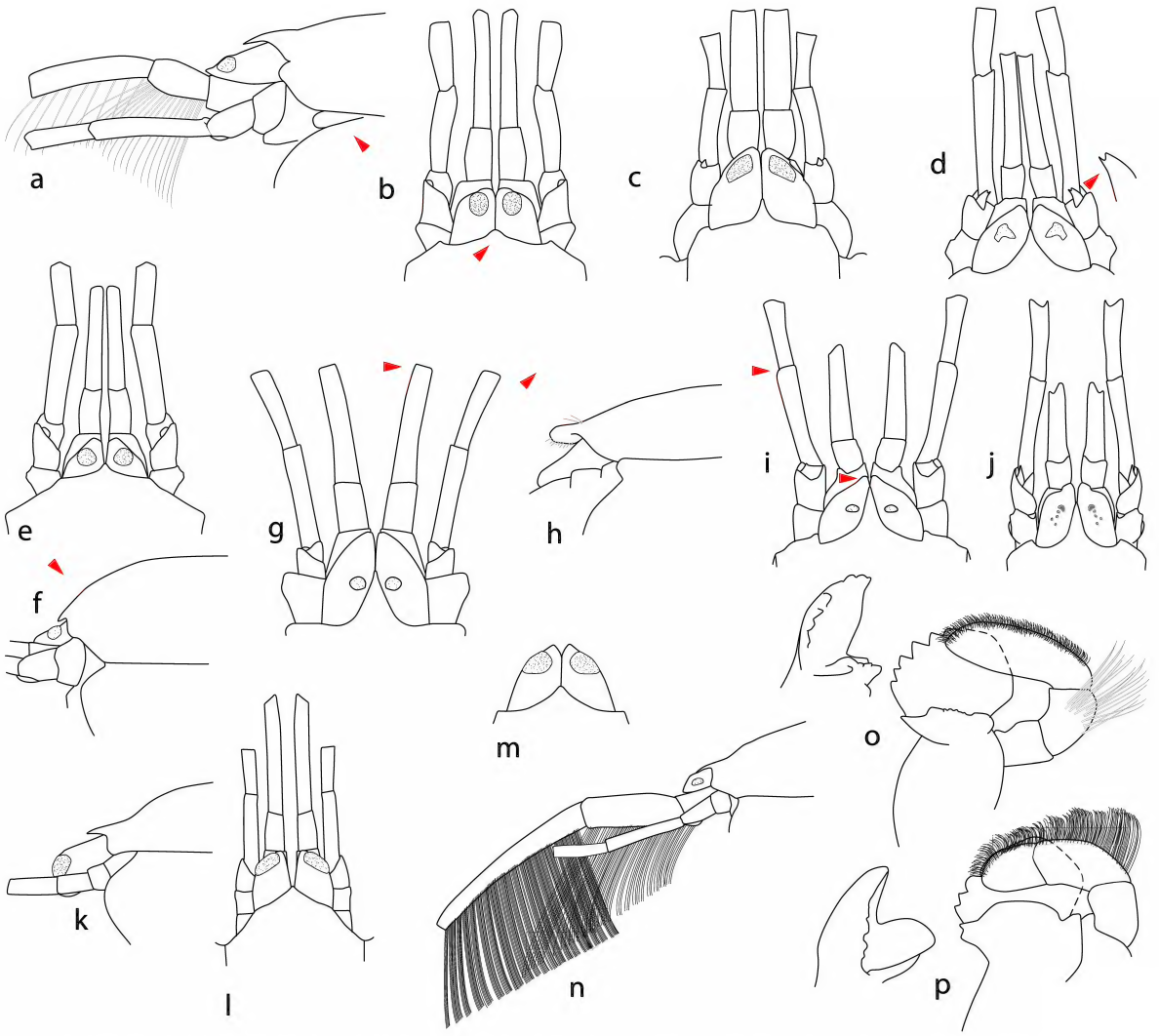

Figure 6. Diagnostic characters for genera of Callianassidae. Anterior carapace, eyestalks, antennules, antennae: a, *Aqaballianassa*; b, *Arenallianassa*; c, *Caviallianassa*; d, *Coriollianassa*; e, f, *Filhollianassa*; g, *Jocullianassa*; h, *Notiax* i, *Praedatrypaea*; j, *Pugnatrypaea*; k, l, *Rayllianassa*; m, *Rudisullianassa*; n, *Trypaea*. Mandible, mesial and lower views: o, *Callianassa*; p, *Rayllianassa*.

Original illustrations: a, *Aqaballianassa lewtonae*, MNHN-IU-2016-8152; c, *Caviallianassa* FP-11, UF 29204; j, *Pugnatrypaea* GMX, USNM 1559553 (ULLZ 17962); o, *Callianassa subterranea*, NMV J16779; p, *Rayllianassa amboinensis*, MNHN-IU-2014-2778.

Cheraminae Manning and Felder, 1991: 780.—Tudge et al., 2000: 136.

Lipkecallianassinae Sakai, 2005: 212.

Lipkecallianassidae Sakai, 2011: 521.

Diagnosis. Rostrum flat, short, triangular, shorter than eyestalks, *or* spike-like, longer than wide; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica oblique in lateral view; anterior branchiostegal margin sinusoidal or semicircular; ***anterior branchiostegal lobe sclerotised, merging smoothly with anterodorsal branchiostegal angle***; posterior margin of carapace without lateral lobes, pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite rudimentary. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. ***Maxilliped 1 epipod truncate, without anterior lobe.*** Maxilliped 3 dactylus slender, digitiform, with setae irregularly spaced along all margins. Cheliped merus

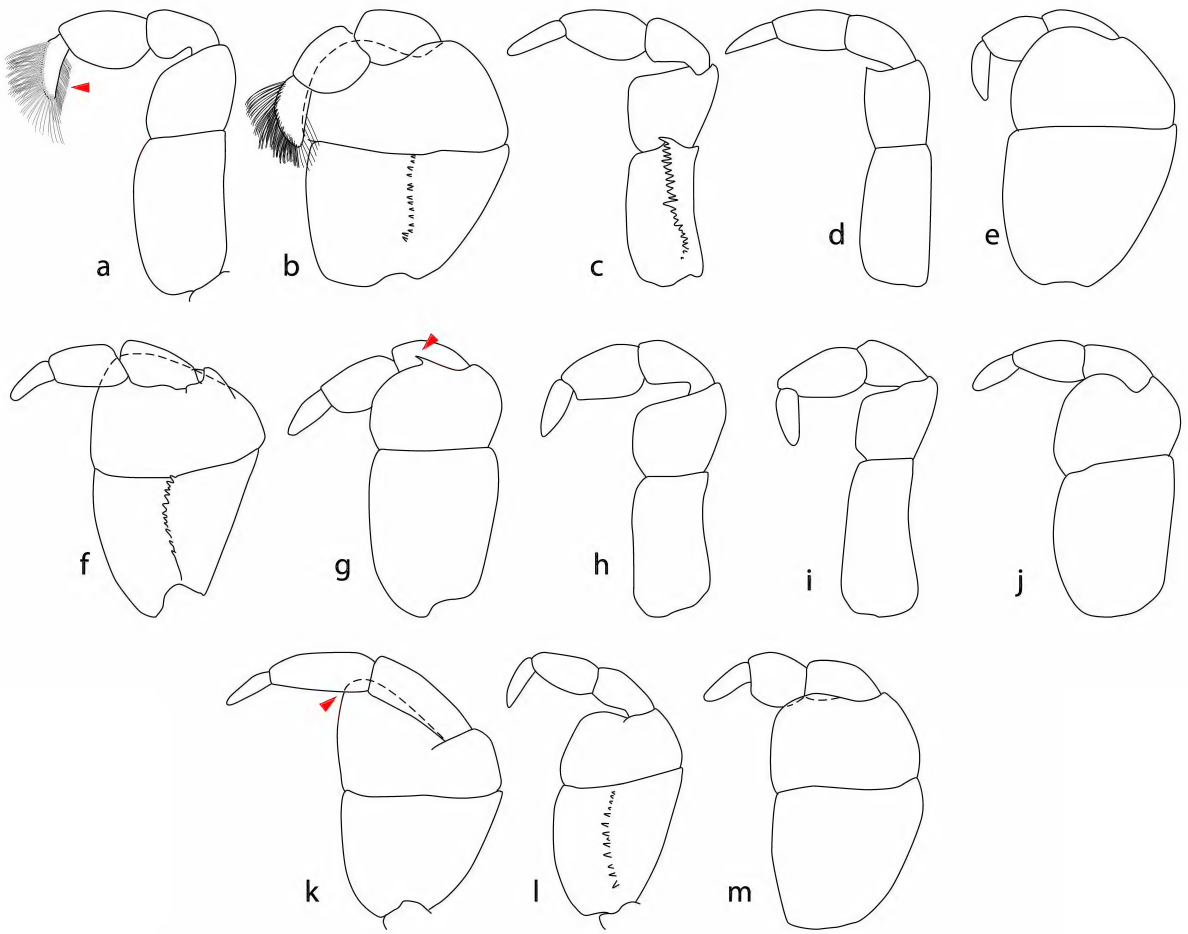

Figure 7. Diagnostic characters for genera of Callianassidae. Maxilliped 3: a, *Callianassa*; b, *Caviallianassa*; c, *Cheramoides*; d, *Lipkecallianassa*; e, *Necallianassa*; f, *Neotrypaea*; g, *Praedatrypaea*; h, *Pugnatrypaea*; i, *Scallasis*; j, *Spinicallianassa*; k, *Trypaea*; l, *Arenallianassa*; m, *Biffarius*.
Original illustrations: a, *Callianassa*; b, *Caviallianassa*; c, *Cheramoides*; d, *Lipkecallianassa*; e, *Necallianassa*; m, *Biffarius delicatulus*, NHMW 25542.

lower margin smooth, *or* with prominent proximal tooth; major cheliped with distinctively flattened palm, sometimes with strong crest above and below. Pereopod 3 propodus wide, with proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate or subchelate. ***Female pleopod 2 rami styliform; endopod much longer than wide, or absent***. Pleopods 3–5 with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae elongate, much longer than wide, *or* reduced and almost embedded in mesial margin of endopod. Uropodal exopod with elevated dorsal plate.

Remarks. Callianassidae differs from its sister taxon Callichiridae in having the rami of the female pleopod 2 styliform and lacking an appendix interna, often absent in the male, rather than broad and often with an appendix interna, and the truncate epipod on maxilliped 1, whereas an anterior lobe runs alongside the exopod in Callichiridae.

The clades resolved in the molecular analysis of over 50 species (Robles et al., in press) bore little resemblance to existing classifications. This necessitated the acceptance of 14 existing genera, the creation of 12 new genera and the synonymy of others. All 26 can be differentiated using morphological features, some of which had been overlooked in earlier accounts. The following key does not reflect phylogeny but attempts to eliminate the most distinctive genera first.

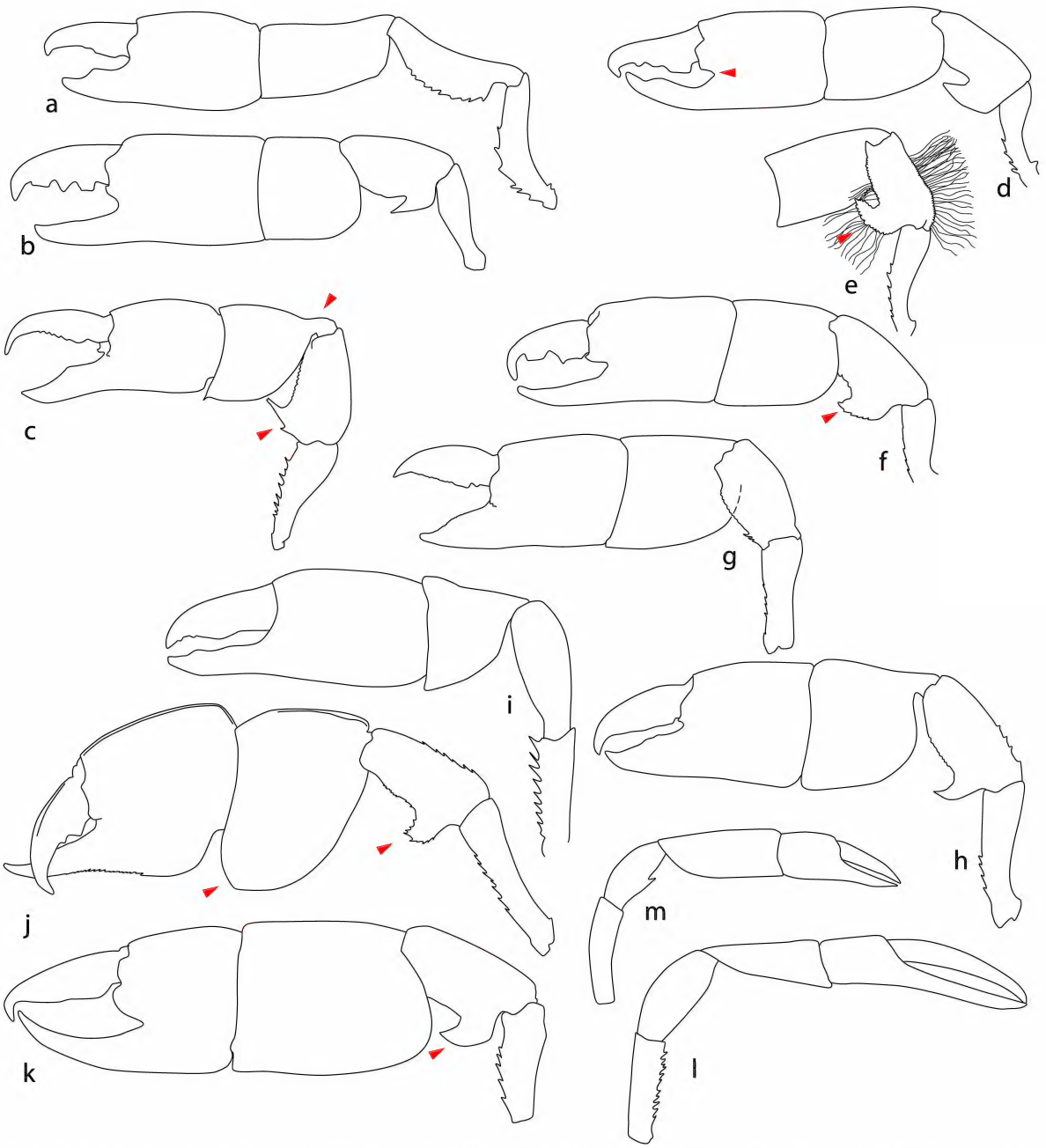

Figure 8. Diagnostic characters for genera of Callianassidae. Male major cheliped: a, *Cheramus*; b, *Fragillianassa*; c, *Coriollianassa*; d, e, *Biffarius*; f, *Arenallianassa*; g, *Caviallianassa*; h, *Callianassa*; i, *Cheramoides*; j, *Filhollianassa*; k, *Gilvossius*. Minor cheliped: l, *Cheramoides*; m, *Neotrypaea*.

Original illustrations: c, *Coriollianassa* MOZ-33, MNHN-IU-2008-10314; e, *Biffarius biformis*, NMV J20793; g, *Caviallianassa* FP-11, UF 29204; j, *Filhollianassa filholi*, NMV J62111.

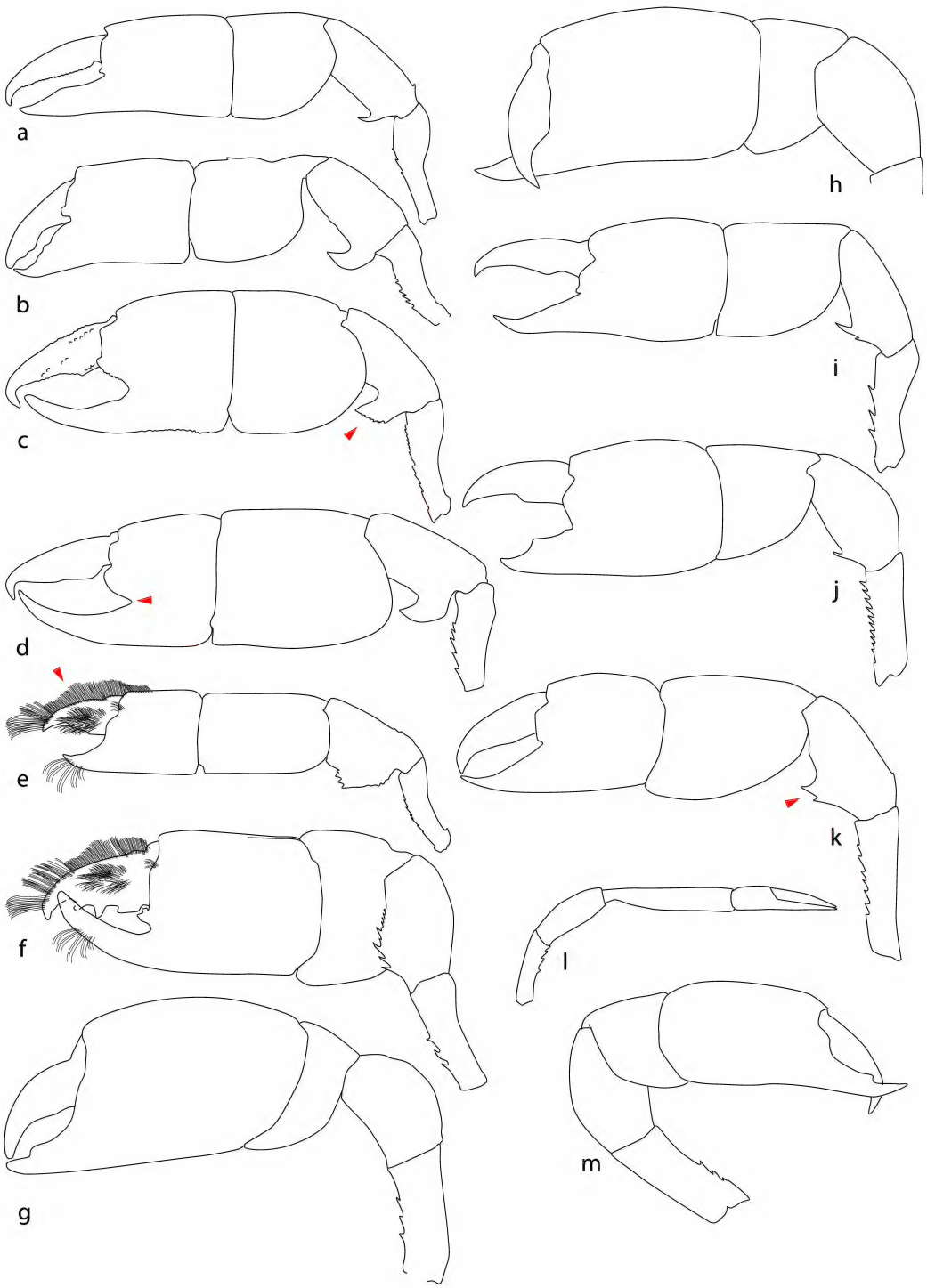

Figure 9. Diagnostic characters for genera of Callianassidae. Male major cheliped: a, *Jocullianassa*; b, *Notiax*; c, *Necallianassa*; d, *Neotrypaea*; e, f, *Paratrypaea*; g, *Raylianassa*; h, *Rudisullianassa*; i, *Scallasis*; j, *Spinicallianassa*; k, *Tastrypaea*. Minor cheliped: l, *Jocullianassa*; m, *Rudisullianassa*.

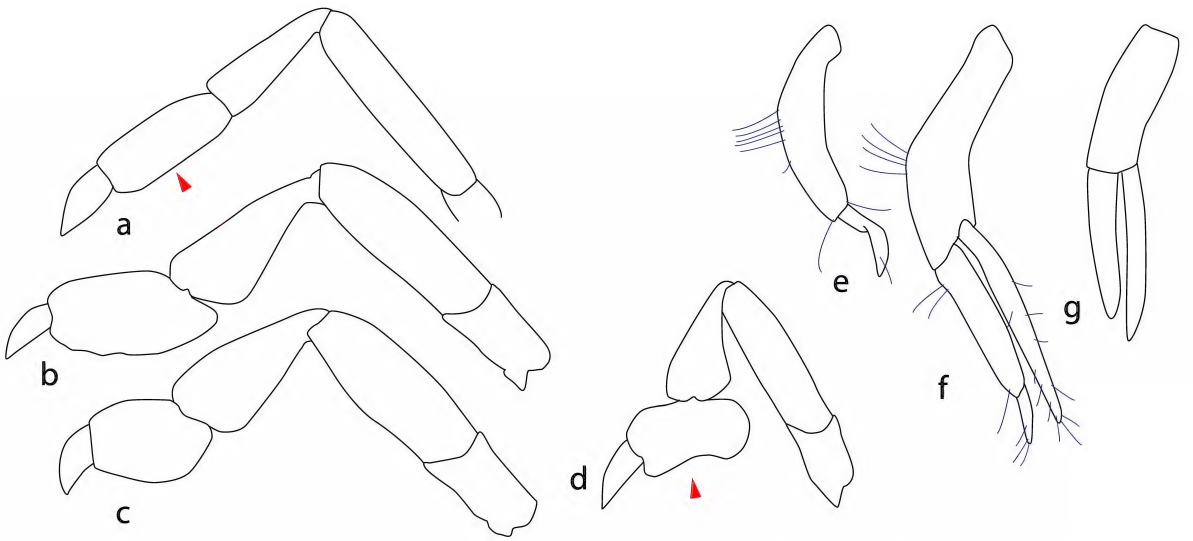

Figure 10. Diagnostic characters for genera of Callianassidae. Pereopod 3: a, *Lipkecallianassa*; b, *Scallasis*; c, *Spinicallianassa*; d, *Jocullianassa*. Male pleopod 1: e, *Caviallianassa*. Male pleopod 2: f, *Caviallianassa*; g, *Poti*.
Original illustration: e, f, *Caviallianassa* FP-11, UF 29204.

Key to genera of Callianassidae

1. Antennular peduncle about 4 times the width of both eyestalks, twice as long as antennal peduncle, with 2 dense rows of adjacent long setae on lower surface (fig. 6n); maxilliped 3 merus produced as massive triangular lobe alongside palp (fig. 7k) ..... *Trypaea*

– Antennular peduncle at most 3 times the width of both eyestalks, with at most bands of scattered long setae on lower surface (fig. 6a); maxilliped 3 merus distally convex at most 2

2. Small triangular sclerite present on branchiostegite at anterior end of linea thalassinica (fig. 6a) ..... *Aqaballianassa*

– Without triangular sclerite on branchiostegite at anterior end of linea thalassinica (figs 6f, k, h) 3

3. Telson tapering, posterior margin with medial spine in deep notch (figs 11g, o) 4

– Telson posterior margin convex, truncate or at most with shallow medial concavity, sometimes with small medial spine 5

4. Maxilliped 3 merus almost rectangular, distally truncate with squarish angle between distal and lower margins (fig. 7d); pereopod 3 propodus linear, without lobe on lower margin (fig. 10a); uropodal exopod distal margin with anterodistal angle obtuse; telson with pair of broad posterior lobes, widely excavate at midpoint (fig. 11g) ..... *Lipkecallianassa*

– Maxilliped 3 merus distally oblique with obtuse angle between distal and lower margins (fig. 7h); pereopod 3 propodus oval, lower margin slightly convex, leading to narrow, distinctly rounded proximal lobe; uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled; telson tapering over distal third to pair of posterior lobes separated by deep notch (fig. 11o) ..... *Pugnatrypaea*

5. Antennular peduncle exceeded by all or most of antennal peduncular article 5 (figs 6d, i) 6

– Antennular peduncle as long as or longer than antennal peduncle (figs 6b, c, e, l) 10

6. Maxilliped 3 merus with spine on distal free margin (fig. 7g); proximolateral lobe of telson prominent, defined posteriorly by clear unchitinised region (fig. 11n) ..... *Praedatrypaea*

– Maxilliped 3 merus without spine on distal free margin; proximolateral lobe of telson prominent or not, indefinitely defined posteriorly 7

7. Major cheliped carpus articulating by means of a short neck with merus, merus with bifid proximal spine (fig. 8c); scaphocerite bifid (fig. 6d) ..... *Coriollianassa*

– Major cheliped carpus without neck, lower margin evenly curved, merus lower margin simple, with simple spine or blade; scaphocerite simple 8

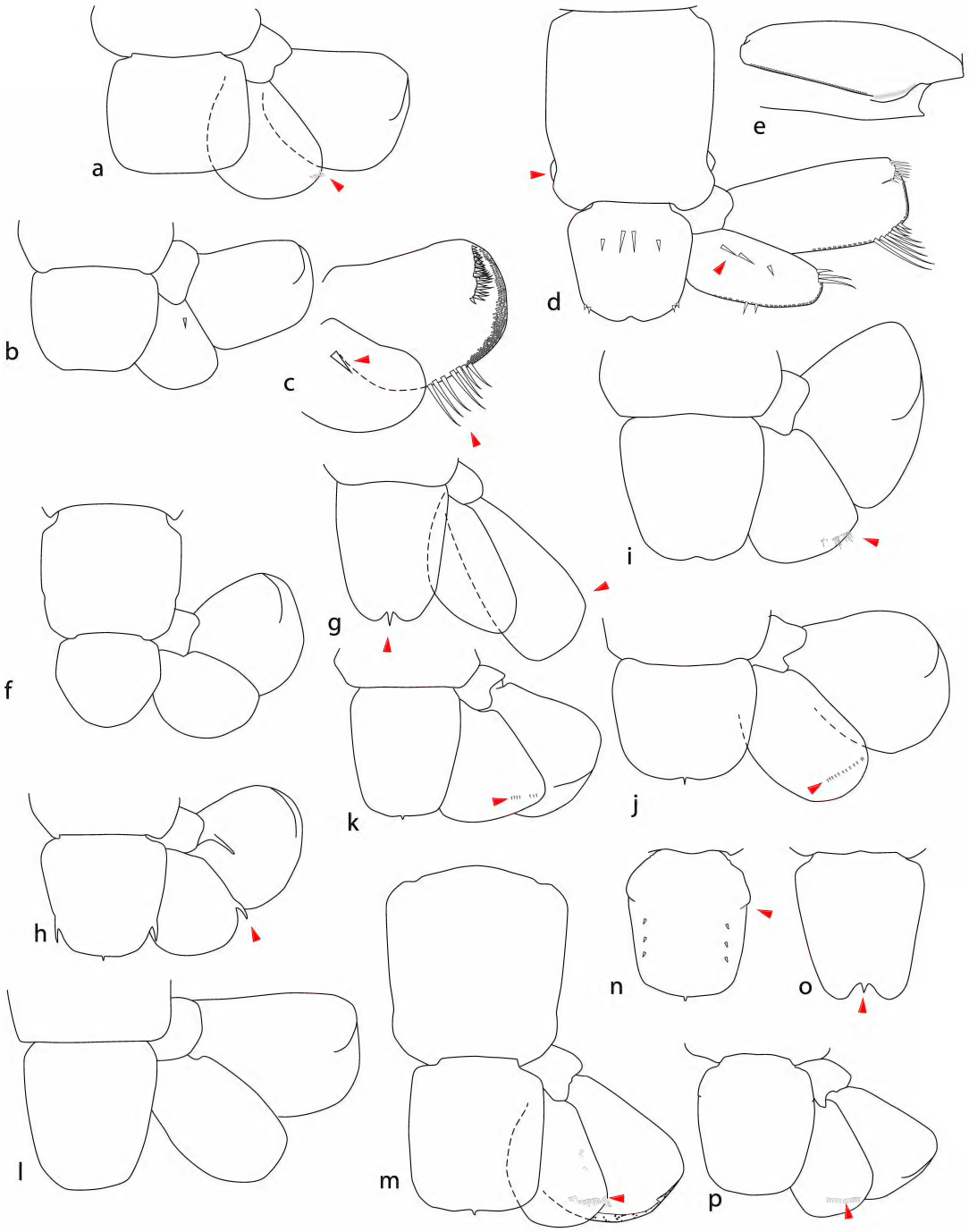

Figure 11. Diagnostic characters for genera of Callianassidae. Pleomere 6, telson, uropod: a, *Arenallianassa*; b, c, *Caviallianassa* (uropod in detail); d, e, *Cheramoides* (with pleomere 6 lateral); f, *Gilvossius*; g, *Lipkecallianassa*; h, *Necallianassa*; i, *Neotrypaea californiensis*; j, *N. petalura*; k, *Notiax*; l, *Poti*; m, *Paratrypaea*; n, *Praedatrypaea*; o, *Pugnatrypaea*; p, *Tastrypaea*.

Original illustrations: a, *Arenallianassa arenosa*, NMV J31887; b, c, *Caviallianassa* FP-11, UF 29204; d, e, *Cheramoides marginata*, MNHN-IU-2016-2462; i, *Neotrypaea californiensis*, NMV J20600; i, *N. petalura*, NMV J59981; k, *Notiax brachyophthalma*, NMV J58880; m, *Paratrypaea maldivensis*, UF 28781.

8. Major cheliped upper margins of ischium and merus, lower margins of merus and carpus beaded, with dense row of fine setae, propodus with deep notch at base of fingers (figs 8d, e) ..... *Biffarius*

– Major cheliped upper margins of ischium and merus, lower margins of merus and carpus smooth, with few well-spaced setae, propodus without deep notch at base of fingers 9

9. Rostrum acute, as long as eyestalk (fig. 6i); cornea diffuse; maxilliped 3 longer than wide at ischium-merus suture (fig. 7c); major and minor chelipeds similar, with saw-tooth blade on lower margin of merus, upper margin concave (fig. 8a); pleomere with sublateral ventral sharp ridge, flared posteriorly (figs 11d, e) ..... *Cheramus*

– Rostrum obtusely triangular, not reaching cornea (fig. 6m); cornea well defined; maxilliped 3 wider at ischium-merus suture than long (fig. 7m); major and minor chelipeds dissimilar, merus unarmed or with small teeth (figs 8h, m); pleomere without sublateral ventral sharp ridge ..... *Rudisullianassa*

10. Rostrum acute, reaching beyond cornea (figs 6g, i) 11

– Rostrum obsolete or triangular, not reaching cornea (figs 6b–f, h, l, m) 15

11. Pereopod 3 propodus bean-shaped, lower margin concave, with broadly rounded proximal lobe (fig. 10d); major cheliped merus with simple perpendicular proximal spine (fig. 9a) ..... *Jocullianassa*

– Pereopod 3 propodus oval or with straight lower margin (Figs 10b, c); major cheliped merus smooth (fig. 8i), *or* with spine (fig. 9h), *or* with blade (figs 9i, j) 12

12. Maxilliped 3 almost rectangular, distally truncate with squarish angle between distal and lower margins (fig. 7c); major cheliped merus without prominent hooked blade (unknown in *Poti*; fig. 8i) 13

– Maxilliped 3 distally convex, extending beyond articulation of carpus (fig. 7j), *or* distally oblique with obtuse angle between distal and lower margins (fig. 7i); major cheliped merus with prominent hooked blade (figs 9i, k) 14

13. Uropodal exopod at least twice as long as wide (fig. 11d); pleopod 2 absent in male ..... *Cheramoides*

– Uropodal exopod about as long as wide (fig. 11l); pleopod 2 present in male (fig. 10g) ..... *Poti*

14. Maxilliped 3 merus wider at ischium-merus suture than long, distally convex, extending only slightly beyond articulation of carpus (fig. 7j); male major cheliped merus with oblique spine about one third or half-way along lower margin, propodus swollen, longer than carpus (fig. 9j); pereopod 3 propodus subrectangular (fig. 10c) ..... *Spinicallianassa*

– Maxilliped 3 merus longer than wide at ischium-merus suture, distally oblique with obtuse angle between distal and lower margins (fig. 7i); male major cheliped merus with 1 or 2 proximal similar teeth and distal denticles on lower margin, propodus narrow, shorter than carpus (fig. 9i); pereopod 3 propodus oval (fig. 10b) ..... *Scallasis*

15. Major cheliped with dorsodistolateral propodus and lateral dactylus with dense brush of setae (figs 9e, f); uropodal endopod with facial distal transverse row of short spiniform setae (fig. 11m) ..... *Paratrypaea*

– Major cheliped with dorsodistolateral propodus and lateral dactylus sparsely setose; uropodal endopod sometimes with facial spiniform setae but not as obvious transverse row 16

16. Anterior carapace strongly depressed by about 45° in lateral view, rostrum blunt (figs 6e, f) ..... *Filhollianassa*

– Anterior carapace moderately or not depressed in lateral view (fig. 6h) 17

17. Antennular peduncle exceeding antennal peduncle by about half length of article 3 (fig. 6l); major and minor chelipeds similar, merus without prominent hook or spine on lower margin, carpus and propodus ovoid in cross-section, upper and lower margins not carinate, carpus of both shorter than upper margin of propodus (fig. 9g); mandibular molar dominating, calcified, swollen projection without sharp edge, incisor without teeth (fig. 6p) ..... *Raylianassa*

– Antennular peduncle about as long as or a little longer than antennal peduncle (figs 6b, c); chelipeds dissimilar, major cheliped merus with prominent hook or spine on lower margin, carpus and propodus flattened, upper and especially lower margins carinate, submarginal mesial face slightly concave (figs 8b, g); minor cheliped carpus longer than upper margin of propodus (fig. 8m); mandibular molar with simple sharp margin, incisor toothed (fig. 6o) 18

18. Maxilliped 3 dactylus with dense brush of long setae over most of upper-distal margin, few setae along lower margin (fig. 7b) 19

– Maxilliped 3 dactylus with scattered setae over upper margin, dense brush of short setae distally on lower margin (fig. 7a) 20

19. Male and female major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base, with deep notch at base of fingers (fig. 8b); pleopod 1 present in male, pleopod 2 absent in male; uropodal endopod without facial spiniform setae ..... *Fragillianassa*

– Male major cheliped merus with 3 oblique similar short proximal spines on lower margin, beaded beyond (fig. 8g), female with simple hook; pleopods 1 and 2 present in male (figs 10e, f); uropodal endopod with at least 1 facial spiniform seta (figs 11b, c) ..... *Caviallianassa*

20. Maxilliped 3 merus longer than width at ischium-merus suture, distally oblique with obtuse angle between distal and lower margins (see above; fig. 7a); male major cheliped merus with simple proximal hook on lower margin (fig. 8h) ..... *Callianassa*

– Maxilliped 3 merus wider at ischium-merus suture than long, distally convex, extending beyond articulation of carpus (figs 7e, f); male major cheliped merus with prominent complex truncate hook (figs 8f, k, 9c) 21

21. Uropodal endopod anterior margin with distal spine (fig. 11h); telson usually with 1 or 2 pairs of lateral spines ..... *Necallianassa*

– Uropodal endopod anterior margin and telson lateral margin without spines (figs 11f, i, j) 22

22. Telson wider than long, posterior margin semicircular (fig. 11f) or subtruncate; uropodal endopod without facial spiniform setae ..... *Gilvossius*

– Telson as wide as long as or longer than wide, posterior margin truncate, slightly concave or slightly convex between posterolateral angles; uropodal endopod with short distal transverse row of facial spiniform setae (figs 11i–k, p) 23

23. Male major cheliped merus with dentate blade at midpoint (fig. 9k); uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin (fig. 11c) ..... *Tastrypaea*

– Male major cheliped merus with prominent basal truncate tooth (figs 8f, 9b, d); uropodal exopod distal and posterior margins densely setose, without blade-like setae 24

24. Rostrum acute, anteriorly directed, with ventral broad swelling (fig. 6h); maxilliped 3 crista dentata absent or comprising few proximal denticles; male major cheliped with distal margin of propodus bearing tooth at base of dactylus (fig. 9b); uropodal endopod distal margin well differentiated from anterior margin, distal margin truncate; telson longer than wide, tapering from base (fig. 11k) ..... *Notiax*

– Rostrum flat against eyestalks (fig. 6b); maxilliped 3 crista dentata consisting of a row of denticles (fig. 7f); male major cheliped with distal margin of propodus having deep notch at base of fingers (fig. 9d); uropodal exopod distal margin well or poorly differentiated from anterior margin; telson wider than or about as wide as long 25

25. Maxilliped 3 merus distally convex, extending only slightly beyond articulation of carpus (fig. 7l); telson wider than long, posterior margin as wide as base, weakly convex between rounded posterolateral angles (fig. 11a) ..... *Arenallianassa*

– Maxilliped 3 merus expanded distally as rounded lobe beyond articulation with ischium (fig. 7f); telson at least as wide as long, usually wider than long, posterior margin narrower than base, often with median spine (figs 11i, j) ..... *Neotrypaea*

Implicit attributes. Unless indicated otherwise, the following attributes are implicit throughout the generic diagnoses. Gonochoristic. Triangular sclerite absent from branchiostegite at anterior end of linea thalassinica; anterior carapace almost flat in lateral view. Rostrum flat against eyestalk. Pleomere 6 without sublateral ventral sharp ridge. Cornea well defined, pigmented, eyestalk distal lobes rounded, largely contiguous. Antennular peduncle length about twice width of both eyestalks, about as long as or a little longer than antennal peduncle; articles 2 and 3 with lateral band (3–5 setae wide) of 20–30 irregularly placed long setae along lower margin, and mesial row of shorter setae. Antennal scaphocerite simple, about as long as wide, apically rounded. Mandibular molar flat, with sharp margin; incisor dentate. Maxilliped 3 merus distally convex, extending only slightly beyond articulation of carpus, without distal spine on mesial margin; crista dentata consisting of a row of numerous denticles; dactylus tapering, with scattered setae over upper margin, dense brush of short setae distally on lower margin. Male major cheliped merus with spine or tooth or variously denticulate along lower margin; upper margins of ischium and merus, and lower margins of merus and carpus, smooth with few well-spaced setae; carpus proximal and lower margins evenly convex; carpus and propodus flattened, upper and especially lower margins carinate, submarginal mesial face slightly concave; propodus distal margin unornamented, oblique; upper distal margin of propodus and dactylus with scattered lateral clusters of setae. Minor cheliped slender, considerably narrower than major cheliped; carpus upper margin longer than propodus. Male pleopod 2 present. Uropodal endopod anterior margin unarmed, without facial setae. Uropodal exopod about as long as wide, distal margin poorly differentiated from anterior margin, anterodistal corner rounded, posterodistal margin densely setose, with short spiniform setae along upper margin.

Aqaballianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:27E2FC97-B393-48F5-B69F-83AFD8FF49D7

Type species. Callianassa aqabaensis Dworschak, 2003, by present designation.

Diagnosis. Hermaphrodite. ***Triangular sclerite separate from branchiostegite at anterior end of linea thalassinica.*** Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided, *or* with weak transverse ridge. Pleomere 6 with sublateral ventral sharp ridge, flared posteriorly. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Mandibular molar calcified, swollen projection without sharp edge; incisor with few teeth. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with oblique spine about one third to half-way along lower margin; propodus distal margin with small lateral tooth; dactylus with dense setae along upper margin. Minor cheliped two-thirds width of major cheliped, both flattened. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 present or absent. Uropodal endopod ovoid, usually longer than wide,

anterior margin straight or slightly convex, posterodistal margin evenly convex, with spiniform setae near anterior and distal margins, *or* with facial spiniform setae on rib. Uropodal exopod 1.0–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson anterolateral lobe obsolete, undefined; truncate or slightly convex between posterolateral angles, *or* slightly concave, sometimes with medial spine.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. The genus is recognisable by the unique triangular sclerite separated by a clear suture or discontinuity from the branchiostegite at the anterior end of the linea thalassinica. All specimens of *A. aqabaensis* have male and female gonopores, but pleopods 1 and 2 are sexually dimorphic (Dworschak, 2003; Markham and Dworschak, 2005). Two species are included besides the type species, *A. brevirostris* from Thailand and *A. lewtonae* from Queensland, plus an undescribed species from Papua New Guinea.

Arenallianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:7A9C78DE-06CA-4407-BA4A-0A2BA6258BDE

Type species. Callianassa arenosa Poore, 1975, by present designation.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse ridge. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. ***Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex***, with facial distal transverse row of short spiniform setae (reduced). Uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled. ***Telson lateral margins convex***.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. Only the type species is known, a common shallow subtidal species in south-eastern Australia. *Arenallianassa arenosa* resembles *Paratrypaea* but lacks the dense setation on the major cheliped of the latter genus and has a prominent truncate meral hook on the major cheliped, whereas *Paratrypaea* has a dentate blade, widest proximally instead. The chelipeds resemble those of species of *Neotrypaea*, a genus defined by a prominent distal lobe on the merus of maxilliped 3, but this is not especially more developed in some species than in *A. arenosa*. The telson is widest at its midpoint, whereas species of *Paratrypaea* and *Neotrypaea* have a tapering telson. *Arenallianassa* differs from *Trypaea* in lacking an extremely long and setose antennule, and differs from *Filhollianassa* in the anterior carapace being flat in profile and the uropodal endopod being ovoid rather than asymmetrical.

Biffarius Manning and Felder, 1991

Biffarius Manning and Felder, 1991: 769–771.—Poore, 2004: 181 (partim).

Trypaea.—Sakai, 2011: 385–387 (partim; not *Trypaea* Dana, 1952).

Type species. Callianassa biformis Biffar, 1971, by original designation.

Diagnosis. ***Rostrum obsolete or obtusely triangular, flat, not reaching cornea***. Pleomere 1 tergite undivided or with weak transverse ridge. Antennular peduncle exceeded by most to all of antennal peduncular article 5; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along the lower margin. Maxilliped 3 merus wider at ischium-merus suture than long; crista dentata absent (or few proximal spines only). Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; upper margins of ischium and merus, and ***lower margins of merus and carpus beaded, with dense row of long fine setae***; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 present or absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson longer than wide, tapering evenly from near base; anterolateral lobe defined posteriorly by short transverse slit; transverse ridge with only fine setae; truncate or slightly convex between posterolateral angles.

Remarks. Biffarius has been widely misused by several authors, with up to a dozen species allocated to it, possibly because it was a genus of last resort in Poore's (1994) key. In fact, the type species shares with one other species, *B. limosus*, and possibly *B. delicatulus*, a long antennal peduncle and the lower margins of the major cheliped merus and carpus being beaded and with a dense row of long fine setae. *Biffarius biformis* occurs from the North Atlantic to Caribbean waters, *B. delicatulus* occurs in the South Atlantic and *B. limosus* is known from south-eastern Australia, a somewhat enigmatic generic distribution.

Callianassa Leach, 1814

Callianassa Leach, 1814: 386, 400.—Sakai, 2011: 359 (comprehensive synonymy).

Type species. Cancer (*Astacus*) *subterraneus* Montagu, 1808, by original designation and monotypy.

Diagnosis. ***Rostrum obsolete or obtusely triangular, flat, not reaching cornea.*** Pleomere 1 tergite undivided or with weak transverse ridge. ***Maxilliped 3 merus distally oblique with obtuse angle between distal and lower margins***, longer than wide at ischium-merus suture. Male major cheliped merus with simple proximal hook on lower margin. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 rarely present. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex or asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin. Uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled.

Remarks. *Callianassa* differs from *Paratrypaea*, *Arenallianassa*, *Filhollianassa* and *Trypaea*, genera it most resembles in these analyses, in having the telson tapering evenly from near base, the merus of maxilliped 3 longer than wide and tapering, the major cheliped with simple proximal hook on its lower margin and absence of facial setae on the uropodal endopod.

Callianassa has been the common catch-all genus for many species whose systematic position was uncertain. Sakai (2011) restricted the genus to a single species but his diagnosis of few characters could refer to any of numerous callianassid genera. The name *Montagua* Leach, 1814, is sometimes listed as a synonym. *Montagua* appears only in the index of Leach (1814: 436) referring to "Genus 44", *Callianassa* in the main text. *Gebios* Risso, 1822, was treated as a junior synonym of *Callianassa* by Sakai (2011) and in many earlier works. If anything, *Gebios* Risso, 1822, is a synonym of *Gilvossius* and is discussed below.

Caviallianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:9819F120-10C6-496D-80E2-BDDAD3FBAE07

Type species. *Cheramus cavifrons* Komai and Fujiwara, 2012, by present designation.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse ridge. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Maxilliped 3 merus wider at ischium-merus suture than long; ***dactylus ovate, with dense brush of long setae over most of upper-distal margin, few setae along lower margin.*** Male major cheliped merus with 1–3 oblique similar short proximal spines on lower margin, beaded beyond; propodus distal margin unornamented, oblique, *or* with small lateral tooth. ***Minor cheliped two-thirds width of major cheliped, both flattened.*** Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial spiniform setae on rib. Uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson about as wide as long, tapering from anterolateral lobe; anterolateral lobe obsolete, undefined.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. A group of two, possibly three, undescribed species from Papua New Guinea and French Polynesia was revealed by our molecular treatment (Robles et al., in press). Morphological examination revealed these to be similar to *Cheramus cavifrons*, of which only the female is known. The chelipeds are similarly compact in all species and have a row of tubercles on the lower margin of the merus beyond a proximal tooth or series of small short spines. Komai and Fujiwara (2012) did not illustrate the unusual setation of the dactylus of maxilliped 3 but its proportions are otherwise similar to the undescribed species, nor did they illustrate the spiniform setae on the face of the uropodal endopod; both features are generally overlooked.

Caviallianassa shares with two genera related on genetic and molecular evidence (Robles et al., in press) a maxilliped 3 dactylus with a dense brush of long setae over most of the upper-distal margin and few setae along the lower margin. *Caviallianassa* differs from the first, *Rudisullianassa*, in having the antennular peduncle about as long as or a little longer than the antennal peduncle (vs exceeded by all or most of the antennal peduncular article 5) and having a small spine on the merus of the major cheliped (vs smooth). Males and females of *Caviallianassa* are known but only females with male gonopores of *Rudisullianassa* are known. *Caviallianassa* differs from *Fragillianassa* in having a wider minor cheliped, lacking a prominent hook on the merus of the major cheliped and having facial setae on the uropodal endopod.

Cheramoides Sakai, 2011

Cheramoides Sakai, 2011: 362.
Cheramus.—Sakai, 2011: 363–365 (partim).

Type species. *Callianassa marginata* Rathbun, 1901, by original designation and monotypy.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Pleomere 6 with sublateral ventral sharp ridge, flared posteriorly. Cornea with scattered reduced pigmentation. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. Maxilliped 3 merus almost rectangular, distally truncate with squarish angle between distal and lower margins, longer than wide at ischium-merus suture; crista dentata a prominent toothed ridge extending beyond proximal margin of merus. Male major cheliped ***merus without prominent hook or spine on lower margin.*** Minor cheliped slender, narrower than major cheliped, with attenuated curved dactylus, longer than palm. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Male pleopod 2 absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial spiniform setae on rib. ***Uropodal exopod***

twice as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson anterolateral lobe obsolete, undefined; slightly concave, sometimes with medial spine.

Remarks. Cheramoides is unique in that the uropodal exopod is twice as long as wide and much longer than the endopod. The maxilliped 3 merus is rectangular, distally truncate with a squarish angle between the distal and lower margins. Only *C. oblonga* from West Africa and *C. brachytelson* from the Andaman Sea are similar to the type species from the Caribbean deep sea.

Cheramus Bate, 1888

Cheramus Bate, 1888: 30.—Manning and Felder, 1991: 91.—Poore, 1994: 101.—Davie, 2002: 459.—Sakai, 2011: 363–366 (partim).—Komai et al., 2014b: 504–505 (partim).

Callianassa (*Cheramus*).—Borradaile, 1903: 545–546.—De Man, 1928: 26, 95.—Gurney, 1944: 8.

Type species. Cheramus occidentalis Bate, 1888, preoccupied, replaced by *Callianassa profunda* Biffar, 1973, by subsequent designation.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Pleomere 6 with sublateral ventral sharp ridge, flared posteriorly. Cornea with scattered reduced pigmentation. ***Antennular peduncle exceeded by all or most of antennal peduncular article 5***. Maxilliped 3 merus almost rectangular, distally truncate with squarish angle between distal and lower margins, longer than wide at ischium-merus suture; crista dentata a prominent toothed ridge extending beyond proximal margin of merus. Male major cheliped merus with serrate blade over lower margin, upper margin concave. ***Minor and major chelipeds similar, both attenuated, with swollen palms***; carpus upper margin as long as or shorter than propodus. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Male pleopod 2 present. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled. Telson anterolateral lobe obsolete, undefined.

Remarks. Cheramus is similar to *Cheramoides* but differs in having uniquely similar minor and major chelipeds, both attenuated and with swollen palms. Contrary to the views in recent accounts, only the type species agrees with this characterisation. Komai et al. (2014b) explained the complex taxonomic history of the type species but followed Manning and Felder (1991) in including other species, *C. marginatus* (type species of *Cheramoides*), *C. orientalis* and *C. oblonga*. Several other species have been included since 1991 (Komai et al., 2014b), but it has to be concluded from Robles et al.'s (in press) phylogeny, supported by morphology, that these and the 16 species included by Sakai (2011) are a diverse assemblage. Komai et al. (2014b) could list only "possibly diagnostic characters", most of which, in our analyses, are features of more than one genus.

Coriollianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:A26A8A5B-426A-4110-9945-31A8B1F5831B

Type species. Callianassa coriolisae Ngoc-Ho, 2014, by present designation.

Diagnosis. ***Rostrum*** acute, anteriorly directed, as long as eyestalks, ***with a ventral keel***. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Cornea with scattered reduced pigmentation. Antennular peduncle exceeded by all or most of antennal peduncular article 5; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite bifid. Maxilliped 3 merus distally oblique with obtuse angle between distal and lower margins, longer than wide at ischium-merus suture; crista dentata a prominent toothed ridge extending beyond proximal margin of merus. Male major cheliped merus with proximal curved spine on lower margin; carpus ***articulating by means of a short neck with merus***. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Male pleopod 2 present or absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial spiniform setae on rib. Uropodal exopod about 1.5–1.8 times as long as wide, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson anterolateral lobe obsolete, undefined.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. Robles et al. (in press) recognised a well-defined genus on molecular and morphological grounds. Two of the four species included were undescribed. The genus is defined by the sharp anteriorly directed rostrum with a ventral keel, the long antennal peduncle, bifid scaphocerite, the unusual neck at the base of the carpus of the chelipeds and the usually bifid meral tooth on the major cheliped. Ngoc-Ho (2014) recognised the similarity between *C. coriolisae* and *C. sibogae*, notably the characteristic chelipeds, and realised their differences from *Cheramus* where they had been placed.

Filhollianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:9A34F27E-ABF5-46ED-AFE8-BA399225F2C6

Type species. Callianassa filholi A. Milne-Edwards, 1878, by present designation.

Diagnosis. ***Anterior carapace strongly domed, depressed over anterior quarter***. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. Antennular peduncle length about 2.5–3 times the width of both eyestalks. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with prominent truncate hook armed with serrations along

lower margin, excavate laterally at base; ***carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave***; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. Uropodal endopod asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin, with facial distal transverse row of short spiniform setae. Uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson lateral margins convex.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. The two species of *Filhollianassa* from south-eastern Australia and New Zealand are immediately recognisable from the strongly domed anterior carapace and strongly inwardly curved carinate upper and lower margins of the carpus and propodus of the major chelipeds. The major cheliped of *Trypaea australiensis*, also in south-eastern Australia but ecologically separate, is similar but this species has a flat dorsum, much longer and more setose antennule, considerably expanded merus of maxilliped 3 and narrower uropodal endopod.

Fragillianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:CFA11DDC-A9C5-4ACC-AC90-E2C6A5456E82

Type species. Callianassa fragilis Biffar, 1970, by present designation.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. ***Antennular peduncle length about 2.5–3 times the width of both eyestalks***. Antennal scaphocerite reduced to small floating disc. Maxilliped 3 merus wider at ischium-merus suture than long; ***dactylus ovate, with dense brush of long setae over most of upper-distal margin, few setae along lower margin***. Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson truncate, *or* slightly convex between posterolateral angles, *or* slightly concave, sometimes with medial spine.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. Fragillianassa, with two species recognised so far, is most similar to *Necallianassa* and *Neotrypaea*, with which it shares a similar eyestalk, antennule and maxilliped 3 merus. *Fragillianassa* differs from both in having an extremely reduced scaphocerite, a dense brush of long setae over most of the upper-distal margin of the dactylus of maxilliped 3 and an ovoid uropodal endopod longer than wide, more symmetrical than in the other two. *Fragillianassa* differs from *Necallianassa* most obviously in lacking spines on the sides of the telson and on the anterior margin of the uropodal endopod, and it differs from *Neotrypaea* in lacking a transverse facial row of setae on the uropodal endopod.

Gilvossius Manning and Felder, 1992

Gebios Risso, 1822: 243 (type species, *Gebios davianus* Risso, 1822, junior subjective synonym of *Cancer candidus* Olivi, 1792, by monotypy) ***nomen oblitum.***

Gebius Agassiz, 1846: 160 (unjustified emendation of *Gebios* Risso, 1822).

Gilvossius Manning and Felder, 1992: 558.—Sakai, 2011: 372 (partim).

Pestarella Ngoc-Ho, 2003: 475 (type species: *Astacus tyrrhenus* Petagna, 1792, by original designation).

Type species. Gonodactylus setimanus DeKay, 1844, by original designation and monotypy.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Antennular peduncle length about 2.5–3 times the width of both eyestalks, length exceeding narrower antennal peduncle. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 present or absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. ***Telson wider than long, almost semicircular***; *or* rarely posterior margin subtruncate.

Remarks. The genus is recognised by the telson being wider than long, almost semicircular in most species, but rarely subtruncate posteriorly. *Gilvossius* differs from *Trypaea, Arenallianassa* and *Paratrypaea*, which share uropodal exopods with densely setose margins, in lacking a deep notch at the base of the cheliped fingers and lacking a facial distal transverse row of short spiniform setae on the uropodal endopod.

Manning and Felder (1992) and Ngoc-Ho (2003) compared *Gilvossius* and *Pestarella* respectively with *Callianassa*, but this latter genus is only remotely similar in Robles et al.'s (in press) analyses. Both *Pestarella* and *Gilvossius* are in the recent literature. *Gilvossius* was erected for a single species, *Gonodactylus setimanus*, shown by molecular and morphological evidence (Robles et al., in press) to be congeneric with *Gilvossius tyrrhenus*, *G. candidus* and *G. whitei* (Sakai, 1999a). Ngoc-Ho (2003) erected *Pestarella* for the type species (*Astacus tyrrhenus*), *G. candidus* and three others; *Pestarella* is here treated as a subjective junior synonym of *Gilvossius*.

Gebios davianus Risso, 1822, is generally agreed to be a junior subjective synonym of *Cancer candidus* Olivi, 1792. *Gebios*, therefore, could be invoked as a senior subjective

synonym of both *Pestarella* Ngoc-Ho, 2003, and *Gilvossius* Manning and Felder, 1992. However, *Gebios* has never been used as a generic name. Ngoc-Ho (2003) provided a comprehensive synonymy of *Pestarella*, a junior synonym of *Gilvossius*, and its included species. The conditions of the International Code of Zoological Nomenclature Article 23.9.1 required for prevailing usage are met. We therefore invoke International Code of Zoological Nomenclature Article 23.9 and designate *Gebios* Risso, 1822, as *nomen oblitum* and both *Pestarella* Ngoc-Ho, 2003, and *Gilvossius* Manning and Felder, 1992, as *nomina protecta*.

Jocullianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:1AC3D163-8895-45EF-8EC6-E87B435B9FDF

Type species. *Callianassa joculatrix* De Man, 1905, by present designation.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Cornea with scattered reduced pigmentation. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. ***Maxilliped 3 merus tapering, not mesially produced***, longer than wide at ischium-merus suture. Male major cheliped merus with proximal perpendicular spine on lower margin; propodus distal margin with deep notch at base of fixed finger. ***Pereopod 3 propodus bean-shaped***, lower margin concave, leading to broadly rounded proximal lobe. Male pleopod 2 absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson anterolateral lobe obsolete, undefined.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. *Jocullianassa joculatrix* is relatively easily recognised by the combination of its acute rostrum, sharp basal spine on the merus of the major cheliped and the excavate lower margin of the propodus on pereopod 3 (Komai and Tachikawa, 2008). *Jocullianassa joculatrix* is far removed from the type species of *Trypaea*, the genus in which it was included by Sakai (2011). The species is common in collections from the Indo-West Pacific.

Lipkecallianassa Sakai, 2002

Lipkecallianassa Sakai, 2002: 477.—Sakai, 2005b: 212.—Sakai, 2011: 522.

Type species. *Lipkecallianassa abyssa* Sakai, 2002, by original designation and monotypy.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Cornea with scattered reduced pigmentation. ***Maxilliped 3 merus*** almost rectangular, distally truncate with squarish angle between distal and lower margins, longer than wide at ischium-merus suture, ***with acute distomesial angle***. Pereopod 3 propodus linear, without lobe on lower margin. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod about 1.5–1.8 times as long as wide. Telson anterolateral lobe obsolete, undefined; ***posterior margin with pair of broad posterolateral lobes, widely excavate at midpoint, with mesial spine***.

Remarks. The monotypic genus *Lipkecallianassa* is known from a single damaged incomplete specimen of the type species. But based on Sakai's (2002) short description and figures, the species has a linear propodus of pereopod 3, seen elsewhere only in *Praedatrypaea longicauda* and *P. modesta* but neither of these species has a strongly excavate posterior telsonic margin. The telson resembles that of species of *Pugnatrypaea* in having an excavate posterior margin; both genera have a narrow ischium-merus of maxilliped 3. All of these three genera have a tooth or spine on the distal margin of the merus of maxilliped 3 but are not allied in the molecular or morphological trees of Robles et al. (in press).

Necallianassa Heard and Manning, 1998

Necallianassa Heard and Manning, 1998: 883–884.
Trypaea.—Sakai, 2011: 385–387 (partim) (not *Trypaea* Dana, 1952).

Type species. *Necallianassa berylae* Heard and Manning, 1998, by original designation.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea, *or* acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite undivided or with weak transverse step. Antennular peduncle length about 2.5–3 times the width of both eyestalks. Antennal scaphocerite simple, longer than wide, acute. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. Uropodal endopod asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin, ***anterior margin with distal spine***. Uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin.

Remarks. The sharp spine on the anterior margin of the uropodal endopod and usually one or two spines on the lateral margins of the telson uniquely differentiate *Necallianassa* from all other callianassids (Heard and Manning, 1998). *Necallianassa truncata* lacks lateral spines on the telson but the male major cheliped has the same setose propodus and dactylus as *N. acanthura* (cf. Ngoc-Ho, 2003). The genus was synonymised with the very different *Trypaea* by Sakai (2011) without explanation.

Neotrypaea Manning and Felder, 1991

Neotrypaea Manning and Felder, 1991: 711–712.

Nihonotrypaea Manning and Tamaki, 1998: 889–891 (type species, *Callianassa japonica* Ortmann, 1891, by original designation) **syn. nov.**

Pseudobiffarius Heard and Manning, 2000: 70.—Sakai, 2005b: 26 (as synonym of *Callianassa*).—Sakai, 2011: 286 (as synonym of *Trypaea*) (type species, *Pseudobiffarius caesari* Heard and Manning, 2000, by original designation and monotypy) **syn. nov.**

Trypaea.—Sakai, 2011: 385–387 (partim; not *Trypaea* Dana, 1852).

Type species. *Callianassa californiensis* Dana, 1854, by original designation.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. ***Eyestalk distal lobes triangular, apices separate or contiguous, produced and tapering over distal half***. Antennular peduncle length about 2.5–3 times the width of both eyestalks. Maxilliped 3 merus expanded distomesially as rounded lobe beyond articulation with ischium, wider at ischium-merus suture than long. Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. ***Uropodal endopod asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin, with facial distal transverse row of short spiniform setae***. Uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled. Telson lateral margins convex; posterior margin slightly concave, sometimes with medial spine.

Remarks. *Neotrypaea* probably includes more species than any genus of Callianassidae. Species have a triangular distal lobe on the eyestalk, the appendix interna of pleopods 3–5 embedded in the endopod, or only slightly protruding, and the merus of maxilliped 3 projecting as a rounded lobe beyond the articulation of the carpus (Manning and Felder, 1991) but not as much as in *Trypaea*. The uropodal endopod is asymmetrical, at least as wide as long, with the distal margin truncate-convex, at right angles to straight anterior margin.

Manning and Tamaki (1998) differentiated *Nihonotrypaea* with the appendix interna of pleopods 3–5 projecting from the endopod margin from *Neotrypaea*, in which the appendix interna is completely embedded in the margin. The same difference was used for erection of *Pseudobiffarius* by Heard and Manning (2000) but this difference is slight. Two clades were evident in the molecular analyses of Robles et al. (in press) but not in the morphological treatment. Species assigned to *Nihonotrypaea* were reported to differ from *Neotrypaea* in having the antennular peduncle shorter than the antennal peduncle (Lin et al., 2007a) but this is true, or they are of similar lengths, in all species from both genera. Both *Nihonotrypaea* and *Pseudobiffarius* were synonymised with *Trypaea* by Sakai (2011).

Notiax Manning and Felder, 1991

Notiax Manning and Felder, 1991: 772–773.—Sakai, 2005b: 18 (as synonym of *Callianassa*).

Not *Notiax*.—Sakai, 2011: 381–382.

Type species. *Callianassa brachyophthalma* A. Milne-Edwards, 1870, by original designation and monotypy.

Diagnosis. ***Rostrum acute, reaching middle of cornea, with ventral broad swelling***. Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 merus wider at ischium-merus suture than long; crista dentata absent (or few proximal spines only). Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 present or absent. Uropodal endopod asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin, with facial distal transverse row of short spiniform setae. Telson longer than wide, tapering evenly from near base; anterolateral lobe defined posteriorly by short transverse slit; transverse ridge with only fine setae; truncate or slightly convex between posterolateral angles.

Remarks. Manning and Felder (1991) differentiated *Notiax* from other callianassids because of its "rostral spine" but it is not the only genus with this feature. *Notiax* differs, at least as adults, in having a broad swelling under the rostrum not seen in others. The telson is longer than wide, tapering from its base, whereas it is more rectangular in similar genera such as *Neotrypaea* and *Arenallianassa*. The maxilliped 3 merus is not lobed as in *Neotrypaea*.

Sakai (2011) redefined *Notiax* to include, besides the type species, five species here included in *Raylianassa*, *Filhollianassa* and *Biffarius*. His diagnosis included alternate states for the shapes of the maxilliped 3, male pleopods 1 and 2 and the telson. Nothing was given that would unify these five species.

Paratrypaea Komai and Tachikawa, 2008

Paratrypaea Komai and Tachikawa, 2008: 36.—Komai and Fujita, 2014: 5–6.

Gilvossius.—Sakai, 2011: 372–373 (partim).

Type species. *Callianassa* (*Trypaea*) *bouvieri* Nobili, 1904, by original designation.

Diagnosis. Rostrum broadly or sharply triangular, almost or as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Antennular peduncle length about 2.5–3 times the width of both eyestalks. Maxilliped 3 merus wider at ischium-merus suture than long. Male major cheliped merus with blade dentate over lower margin, widest proximally; carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave; propodus distal margin with deep notch at base of fixed finger; ***upper distal margin of propodus and dactylus with dense brush of setae***. Pereopod 3 propodus

rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial distal transverse row of short spiniform setae. Uropodal exopod distal margin differentiated from anterior margin, anterodistal corner rounded or right-angled. Telson longer than wide, tapering evenly from near base; anterolateral lobe defined posteriorly by short transverse slit; transverse ridge with only fine setae; truncate or slightly convex between posterolateral angles.

Remarks. Species of *Paratrypaea* are immediately recognisable by the dense brush of setae on the propodus and lateral dactylus of the major cheliped, and the merus of the male major cheliped having a dentate blade on its lower margin, rather than a hook as in many other genera.

Paratrypaea was synonymised with *Gilvossius* by Sakai (2011) because the two genera share the same type of male pleopods 1 and 2, but the two genera differ in many ways (Komai and Fujita, 2014). *Gilvossius chichijimaensis* Sakai, 2015, was shown to be a junior synonym of *Paratrypaea bouvieri* (see Komai, 2017).

Poti Rodrigues and Manning, 1992

Poti Rodrigues and Manning, 1992a: 9–10.
Callianassa.—Sakai, 1999a: 11–13 (partim).
Cheramus.—Sakai, 2011: 363–365 (partim).

Type species. *Poti gaucho* Rodrigues and Manning, 1992, by original designation and monotypy.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Cornea with scattered reduced pigmentation. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. ***Maxilliped 3 merus almost rectangular, distally truncate with squarish angle between distal and lower margins***, longer than wide at ischium-merus suture; crista dentata a prominent toothed ridge extending beyond proximal margin of merus. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Male pleopod 2 present. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson anterolateral lobe obsolete, undefined.

Remarks. Poti was said to differ from all other callianassid genera in having an incomplete linea thalassinica (Rodrigues and Manning, 1992a), a condition we were unable to confirm. Otherwise, the maxilliped 3 and minor cheliped of the only species resembles those of species of *Cheramoides*. The uropodal exopod is broad, while it is exceptionally long and narrow in *Cheramoides*.

Poti was synonymised with *Callianassa* by Sakai (1999a), along with seven other genera, and with a redefined *Cheramus* by Sakai (2011) who took a broad view of both genera.

***Praedatrypaea* gen. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:CDBA883E-288C-4CDA-80F4-1BEE665FA3D0

Type species. Callianassa praedatrix De Man, 1905, by present designation.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Pleomere 6 with sublateral ventral sharp ridge, flared posteriorly. Antennular peduncle exceeded by all or most of antennal peduncular article 5; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. ***Maxilliped 3 merus*** wider at ischium-merus suture than long, ***with distal spine on distal free margin***. Male major cheliped merus with blade dentate over lower margin, widest proximally. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with spiniform setae near anterior and distal margins. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. ***Telson anterolateral lobe prominent, defined posteriorly by clear unchitinised region***; truncate or slightly convex between posterolateral angles, *or* slightly concave, posterior margin sometimes with medial spine.

Etymology. An alliteration of the name of the type species and *Trypaea*, a genus of the family.

Remarks. The hooked spine on the distal margin of the merus of maxilliped 3 immediately defines *Praedatrypaea*. The genus is also unusual in that the proximolateral lobes at the base of the telson are prominent, especially ventrally, and are defined by a weakly chitinised suture dorsally and laterally. In other genera, these lobes may be evident and defined at most by a narrow slit.

***Pugnatrypaea* gen. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:0F41845B-F526-4AB8-80B7-A60B6538919E

Type species. Callianassa pugnatrix De Man, 1905, by present designation.

Diagnosis. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Cornea with scattered reduced pigmentation. Antennular peduncle from about as long exceeded by all of antennal peduncular article 5; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin.

Maxilliped 3 merus distally oblique with obtuse angle between distal and lower margins, without distal spine on mesial margin. Male major cheliped merus with simple proximal hook on lower margin; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Male pleopod 2 present or absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with spiniform setae near anterior and distal margins, *or* with facial spiniform setae on rib. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. ***Telson anterolateral lobe obsolete, undefined; tapering over distal third to pair of posterior lobes separated by deep notch, with medial spine.***

Etymology. An alliteration of the name of the type species and *Trypaea*, a genus of the family.

Remarks. The telson tapers over its distal third to a pair of lobes separated by a deep notch with a medial spine. The two pairs of spiniform setae typically found on the posterolateral angles of the telson of callianassids are prominently enlarged and displaced anteriorly. *Pugnatrypaea pugnatrix* and an unidentified species *Pugnatrypaea* GMX lie on the same molecular clade (Robles et al. 2019). Both have a simple curved spine on the lower margin of the merus of the major cheliped. The antennular peduncle is shorter than the antennal peduncle in *Pugnatrypaea* GMX (fig. 6j) while they appear to be of similar lengths in *Pugnatrypaea pugnatrix* (De Man, 1928: fig. 23). Species with similar maxillipeds 3, telsons and short antennular peduncles are *P. intermedia* and *P. lobetobensis* but these differ in having a truncate, instead of rounded, uropodal exopod and the merus of the major cheliped dentate along the lower margin and with a spine on the upper margin.

Rayllianassa Komai and Tachikawa, 2008

Rayllianassa Komai and Tachikawa, 2008: 42–43.—Komai and Fujita, 2014: 551–552.

Notiax.—Sakai, 2011: 381 (partim).

Type species. Callianassa amboinensis De Man, 1888, by original designation and monotypy.

Diagnosis. Hermaphrodite. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. ***Eyestalk distal lobes obliquely truncated, apices diverging.*** Antennular peduncle exceeding antennal peduncle by about half length of article 3; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. Mandibular molar calcified, swollen projection without sharp edge, incisor with few teeth. Maxilliped 3 merus wider at ischium-merus suture than long. Male ***major cheliped merus without prominent hook or spine on lower margin; carpus and propodus ovoid in cross-section, upper and lower margins not markedly carinate***; propodus distal margin with small lateral tooth. Minor cheliped about two-thirds width of major cheliped, both swollen; carpus upper margin as long as or shorter than propodus. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial spiniform setae on rib. Uropodal exopod posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson lateral margins convex; anterolateral lobe obsolete, undefined; slightly concave, sometimes with medial spine.

Remarks. Rayllianassa amboinensis is recognisable by the absence of a hook on the merus of the major cheliped, the propodi being swollen and the pair being little different in size. The lobes on the eyestalks are truncate-oblique and the maxilliped 3 particularly broad. Komai et al. (2014a) added a second species *R. rudisulcus* and emended the generic diagnosis to accommodate the presence or absence of a dorsal oval, but the authors were ambivalent about the value of this character in callianassid systematics. This species and another were shown by Robles et al. (in press) to differ on both molecular and morphological criteria (see *Rudisullianassa* below where the two genera are compared).

Rayllianassa amboinensis has been reported from throughout the Indo-West Pacific and illustrated several times since its discovery in Ambon, Indonesia (Komai et al., 2014a; Komai and Tachikawa, 2008; Ngoc-Ho, 2005; Poore and Griffin, 1979; Sakai, 1984, 1988, 1999a). There is considerable discrepancy between the illustrations. Robles et al. (in press) found substantial genetic difference between eight individuals from Papua New Guinea, Philippines and the Line Islands pointing to the probability of more than one species in this genus.

All authors cited above have reported only females with the exception of Sakai (1999a) who reported two males and a female from Ambon, all twice as long as the "female" holotype and other subsequent records. Examination of all the material available to us shows them to be hermaphrodites with both male and female gonopores. Ngoc-Ho (1991) illustrated minute pleopods 1 and 2 on a single male that was renamed *Callianassa ngochoae* by Sakai (1999a) and later synonymised by Komai et al. (2014a). The generic position of *Callianassa ngochoae* is uncertain. Males of species of *Rudisullianassa* and *Spinicallianassa* have also never been reported. All "females" with typical pleopods 1 and 2, including ovigerous individuals, have both female gonopores on coxae of pereopods 3 and male gonopores on coxae of pereopods 5 and are probable hermaphrodites.

Rudisullianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:C2EFC849-6C6B-4466-8B47-9DF66EBF5D46

Type species. Rayllianassa rudisulcus Komai, Fujita and Maenosono, 2014, by present designation.

Diagnosis. ***Hermaphrodite.*** Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. Antennular peduncle

exceeded by all or most of antennal peduncular article 5; articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Maxilliped 3 merus wider at ischium-merus suture than long; dactylus ***ovate, with dense brush of long setae over most of upper-distal margin, few setae along lower margin***. Male major cheliped merus without prominent hook or spine on lower margin; propodus distal margin with small lateral tooth. Minor cheliped about two-thirds width of major cheliped, both swollen; carpus upper margin as long as or shorter than propodus. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with or without facial spiniform setae on rib. Uropodal exopod 1.0–1.8 times as long as wide, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson about as wide as long, tapering from anterolateral lobe; anterolateral lobe obsolete, undefined; posterior margin slightly concave, sometimes with medial spine.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. Komai et al. (2014a) described *Rayllianassa rudisulcus* based on one female; they did not note how the setation on the dactylus of maxilliped 3, which they correctly described as "stout", differed from that of *R. amboinensis*. The form found in *Rayllianassa*, tapering with few long setae on the upper surface and a dense brush of short setae below, is typical of most callianassids. *Rudisullianassa* differs further from *Rayllianassa* in having the antennular peduncle shorter than the antennal peduncle, whereas the opposite is true in *Rayllianassa*, and the minor cheliped is relatively smaller. The atypical maxilliped 3 dactylus seen in *R. rudisulcus* is also seen in *Biffarius*, *Fragillianassa* and *Caviallianassa* but these are gonochoristic genera. *Rudisullianassa rudisulcus* and a second undescribed species were common in collections from Papua New Guinea (Robles et al. 2019). All individuals had both male and female gonopores. Both species were associated with submerged wood.

The unusual maxilliped 3 was initially mistaken by one of us (GCBP) for the form seen in eucalliacids, also with swollen similar chelipeds. In eucalliacids, the dactylus is also extremely setose but in this case the apex is decidedly truncate.

Scallasis Bate, 1888

Scallasis Bate, 1888: 34.—Manning and Felder, 1991: 780.
Callianassa (*Scallasis*).—Borradaile, 1903: 547–548 (partim).
Cheramus.—Sakai, 2011: 363–365 (partim).

Type species. Scallasis amboinae Bate, 1888, by monotypy.

Diagnosis. ***Rostrum acute, anteriorly directed, as long as eyestalks***. Pleomere 1 tergite fused, divided into 2 sections by transverse step. Pleomere 6 with sublateral ventral sharp ridge, flared posteriorly. ***Eyestalk distal lobes acute, apices separate***. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. ***Maxilliped 3 merus distally oblique with obtuse angle between distal and lower margins, longer than wide at ischium-merus suture***; crista dentata a prominent toothed ridge extending beyond proximal margin of merus. Male major cheliped merus with 2 or 3 proximal similar teeth and distal denticles on lower margin; propodus distal margin with small lateral tooth. Pereopod 3 propodus oval, lower margin slightly convex, leading to narrow sharply rounded proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, anterior margin unarmed or with spine at midpoint, with facial spiniform setae on rib. Uropodal exopod 1.0–1.8 times as long as wide, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson lateral margins convex; transverse ridge with fine setae and spiniform setae; posterior margin truncate, *or* slightly convex between posterolateral angles, *or* slightly concave, sometimes with medial spine.

Remarks. We now follow Clark (2018) in attributing this genus to Bate rather than Spence Bate. The holotype of *Scallasis amboinae* was examined (by GCBP) and additional specimens were found in Papua New Guinea, enabling the species to be well characterised. The genus is recognised by the combination of a narrow rostrum, eyestalks with acute apices, a narrow maxilliped 3, a simple or bifid spine on the merus of the major cheliped, and exceptionally strong spiniform setae on the face of the uropodal endopod and on the face of the telson.

Spinicallianassa gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:DCD1DFBE-9DFF-481E-89CA-483A0AC6DDD8

Type species. Cheramus spinicauda Komai, Maenosono and Fujita, 2014, by present designation.

Diagnosis. Hermaphrodite. Rostrum acute, anteriorly directed, as long as eyestalks. Pleomere 1 tergite undivided or with weak transverse step. Pleomere 6 with or without sublateral ventral sharp ridge, flared posteriorly. Antennular peduncle articles 2 and 3 with single lateral row of 6–10 well-spaced long setae along lower margin. Antennal scaphocerite simple, longer than wide, acute. Mandibular molar calcified, swollen projection without sharp edge, incisor with few teeth. Maxilliped 3 merus wider at ischium-merus suture than long. ***Male major cheliped merus*** with oblique spine one third to half-way along lower margin; ***dactylus with dense setae along upper margin***. Minor cheliped two-thirds width of major cheliped, both flattened. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with spiniform setae near anterior and distal margins, *or* on rib. Uropodal exopod about 1.5–1.8 times as long as wide, distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. ***Telson about as wide as long, tapering from anterolateral lobe***;

anterolateral lobe obsolete, undefined; transverse ridge sometimes with spiniform setae; posterior margin slightly concave, sometimes with medial spine.

Etymology. An alliteration of the name of the type species and *Callianassa*, type genus of the family.

Remarks. Species of *Spinicallianassa* have dense setae on the upper margin of the dactylus of the male major cheliped, approaching that of *Paratrypaea* but differing from this genus in many ways, notably having a small meral spine on the major cheliped rather than a prominent toothed blade. The row of short spiniform setae along the posterior margin of the telson may be characteristic of this genus only. *Spinicallianassa* shares with *Aqaballianassa* and *Rayllianassa* a dominating calcified mandibular molar without a sharp edge and an incisor without teeth.

Tastrypaea gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:B5299239-C36C-4B78-8A7A-BB82710B67B5

Type species. *Callianassa poorei* Sakai, 1999, herein designated.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 merus wider at ischium-merus suture than long. ***Male major cheliped merus with 1 or 2 small teeth just before midpoint***; carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave; propodus distal margin with deep notch at base of fixed finger. Minor cheliped two-thirds width of major cheliped, both flattened. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. ***Uropodal endopod asymmetrical, at least as wide as long, distal margin truncate-convex, at right angles to straight anterior margin***, with facial distal transverse row of short spiniform setae. Uropodal exopod distal margin clearly differentiated from anterior margin, anterodistal corner right-angled, posterodistal margin with row of 6–8 long blade-like setae proximal to long setae on distal margin. Telson lateral margins convex.

Etymology. An alliteration of Tasmania, type locality of the type species, and *Trypaea*, a genus of the family.

Remarks. We have no molecular data to support this genus but *Callianassa poorei* displays several significant morphological differences from its nearest neighbours to justify a new genus (Sakai, 1999b). *Tastrypaea* resembles species of *Paratrypaea* in having a well-developed transverse row of spiniform setae near the anterodistal angle of the uropodal endopod but differs in not having especially setose fingers on the major cheliped. The species also differs from *Paratrypaea* and from *Arenallianassa arenosa*, which has an obsolete row of spiniform setae on the uropodal endopod, in that the chelipeds are not extremely dissimilar, in not having a well-developed blade on the major cheliped, the uropodal endopod being asymmetrical, as wide as long, with its distal margin truncate-convex, at right angles to the straight anterior margin (rather than ovoid and longer than wide) and the uropodal exopod having a row of long blade-like setae proximal to long setae on the distal margin (rather than having densely setose margins). *Tastrypaea* differs from *Filhollianassa*, its sister taxon in Robles et al. (in press), in not having a depressed anterior carapace and chelipeds without prominent marginal crests.

Trypaea Dana, 1852

Trypaea Dana, 1852a: 14.—Poore, 2004: 184.—Sakai, 2011: 385–387 (partim).

Callianassa (*Trypaea*).—Borradaile, 1903: 546 .—De Man, 1928: 27, 96 (partim).

Type species. *Trypaea australiensis* Dana, 1852, by monotypy.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. ***Eyestalk distal lobes obsolete, truncate. Antennular peduncle length about 4 times the width of both eyestalks, twice as long as antennal peduncle; articles 2 and 3 with 2 single similar rows of closely spaced setae laterally and mesially along lower margin, extending on to flagellum***. Maxilliped 3 merus grossly expanded distomesially beyond articulation with ischium, wider at ischium-merus suture than long; crista dentata absent (or few proximal spines only). Male major cheliped merus with prominent truncate hook armed with serrations along lower margin, excavate laterally at base; carpus and propodus flattened, upper and lower margins carinate, blade-like, submarginal mesial face especially of carpus deeply concave; propodus distal margin with deep notch at base of fixed finger. Pereopod 3 propodus rectangular, lower margin deeply convex, leading to broadly rounded free proximal lobe. Male pleopod 2 absent. Uropodal endopod ovoid, usually longer than wide, anterior margin straight or slightly convex, posterodistal margin evenly convex, with facial distal transverse row of short spiniform setae. Telson lateral margins convex; slightly concave, sometimes with medial spine.

Remarks. *Trypaea australiensis* is immediately distinguished from all other callianassids by the massive antennular peduncles, far exceeding the antennal peduncles, bearing on their lower margin a double row of adjacent long setae. The merus of maxilliped 3 is more grossly expanded distally than in any other genus. In all other genera that appear to have setose antennae, the setae are scattered in broad bands and not adjacent. *Trypaea* has only one species which is genetically well separated from its sister taxa (Robles et al. 2019). These are *Arenallianassa* from south-east Australia, *Filhollianassa* from south-east Australia and New Zealand, and the more widespread Indo-West Pacific *Paratrypaea*.

Sakai (1999a) synonymised *Trypaea* and eight other genera with *Callianassa*, and later, Sakai (2005b) added a further two genera to this synonymy. Sakai (2011) revived the genus and synonymised five genera with *Trypaea* based on shared features of the male pleopods 1 and 2, which are poorly developed or absent in all callianassids. In doing so, he included 53 species.

Callianopsidae Manning and Felder, 1991

Figure 12

Callianopsinae Manning and Felder, 1991: 787–789.—Schweitzer Hopkins and Feldmann, 1997: 237.—Sakai, 2005b: 226–227.—Sakai, 2011: 477–478.—Sakai et al., 2015: 122–124.

Callianopsidae.—Sakai, 2011: 477.—Sakai et al., 2015: 121–122.—Dworschak and Poore, 2018: 66–67.

Neocallianopsinae Sakai, 2011: 482.

Bathycalliacinae Sakai and Türkay, 1999a: 204.—Sakai, 2005b: 213–214.—Sakai, 2011: 347–348 **syn. nov.**

Bathycalliacidae Sakai, 2011: 347 **syn. nov.**

Vulcanocalliacinae Dworschak and Cunha, 2007: 37.—Sakai, 2011: 350 **syn. nov.**

Diagnosis. Rostrum flat, short, triangular, shorter than eyestalks, *or* spike-like; median carina absent, *or* on rostrum only; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica horizontal in lateral view; anterior branchiostegal margin sinusoidal or semicircular; anterior branchiostegal lobe simple, scarcely calcified, merging smoothly with anterodorsal branchiostegal angle and anterolateral margin of carapace; posterior margin of carapace without lateral lobes; pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite usually elongate, rarely rudimentary. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. ***Maxilliped 3 dactylus dilating, truncate, with dense field of setae on distal margin***. ***Cheliped merus lower margin spinose, or with small proximal tooth***; palm oval in cross-section, barely crested above or below. Pereopod 3 propodus rectangular or oval, up to twice as long as wide, with proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate. Female pleopod 2 rami narrower and with more reduced setation than pleopods 3–5; endopod flattened and 3–5 times as long as wide. Pleopods 3–5 with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae elongate, much longer than wide. ***Uropodal exopod without elevated dorsal plate***.

Remarks. Callianopsids differ from other callianassoids except eucalliacids in having the dactylus of maxilliped 3 dilating, truncate and with a dense field of setae on its distal margin. The uropodal exopod lacks a dorsal plate, which is present in eucalliacids. Members of the family have lateral ridges on the eyestalks and maxilliped 3 ischium with a strong proximal lobe on the lower margin. These features place the family far removed from Callianassidae, with which it was compared by Sakai (2011).

Callianopsinae was treated as a subfamily of Ctenochelidae by Manning and Felder (1991) and by Schweitzer Hopkins and Feldmann (1997), as a subfamily of Gourretiidae by Sakai (2005b) and as a full family by Sakai (2011).

Dworschak and Poore (2018) showed that *Neocallianopsis* is a synonym of *Callianopsis*, and therefore, Neocallianopsinae Sakai, 2011, is a synonym of Callianopsidae. Bathycalliacinae and Vulcanocalliacinae, both monotypic and originally subfamilies of Callianassidae, were included in Bathycalliacidae, newly elevated to family rank by Sakai (2011). Dworschak and Cunha (2007) noted that the two taxa shared epipods on maxilliped 3 to pereopod 4 (found also in the only species of Paracalliacidae), similar maxillipeds 3, propodi on pereopod 3, telsons and uropods, and blindness. The morphological analysis found the absence of an appendix masculina on male pleopod 2 to be a synapomorphy.

In his discussion of Bathycalliacinae, Sakai (2011) contradicted Dworschak and Cunha's (2007) assertion that the holotype of *Bathycalliax geomar* is a male (as originally stated). Subsequent examination by PCD has shown the original observation was correct. Sakai (2011) erroneously stated that the male pleopod 1 is absent and that *Vulcanocalliax arutyunovi* possesses a dorsal plate on the uropodal exopod, again not true.

The molecular analysis of Robles et al. (in press) found one bathycalliacid representative, *Vulcanocalliax arutyunovi*, to be a sister taxon to one example of Callianopsidae, *Callianopsis goniophthalma*, a result consistent with the morphological analysis that found *Bathycalliax* to be closely allied. On the basis of this evidence, we synonymise Bathycalliacidae with Callianopsidae and move Vulcanocalliacinae to Callianopsidae without recognising subfamilies.

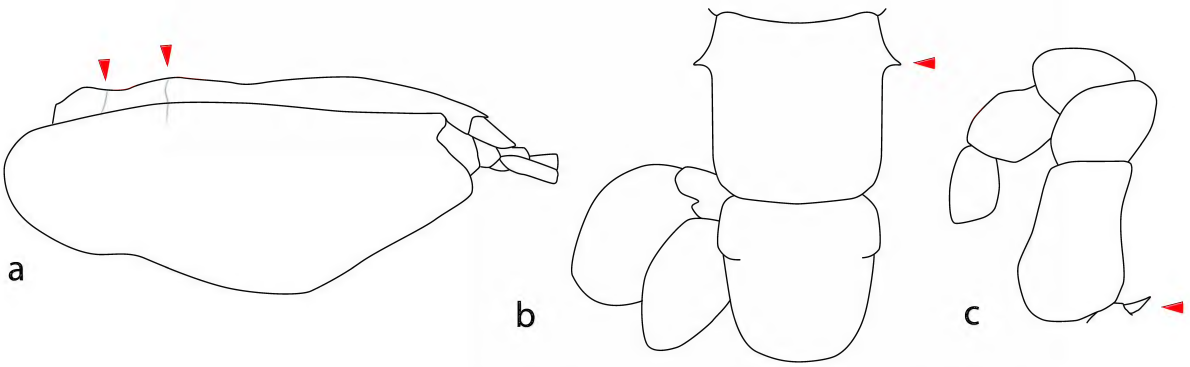

Figure 12. Diagnostic characters for genera of Callianopsidae. Carapace: a, *Bathycalliax*. Pleomere 6: c, *Callianopsis*. Maxilliped 3: c, *Bathycalliax*.

Key to genera of Callianopsidae

1. Pleomere 6 with prominent lateral projections (fig. 12b); carapace with longitudinal carina running from rostrum; epipods absent ..... *Callianopsis*

– Pleomere 6 without prominent lateral projections; carapace without longitudinal carina; epipods present on maxilliped 3 to pereopod 4 2

2. Two cardiac sulci present (fig. 12a); maxilliped 3 with rudimentary exopod (fig. 12c) ..... *Bathycalliax* (1 species, *B. geomar*)

– Cardiac sulci absent; maxilliped 3 exopod absent ..... *Vulcanocalliax* (1 species, *V. arutyunovi*)

Bathycalliax Sakai and Türkay, 1999

Bathycalliax Sakai and Türkay, 1999: 204.—Sakai, 2005b: 214.—Sakai, 2011: 349.

Type species. Bathycalliax geomar Sakai and Türkay, 1999, by original designation and monotypy.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea; carapace without median carina; ***cardiac sulci present***. Pleomere 6 without lateral projections. Maxilliped 3 exopod present. Male major cheliped merus lower margin straight, with proximal row of denticles.

Remarks. Bathycalliax geomar is the sole species, placed by its authors in its own callianassid subfamily, Bathycalliacinae. Dworschak and Cunha (2007) confirmed that the holotype male pleopod 1 has a unique flagellate article 2 but that the smaller male paratype lacks pleopod 1. Sakai (2011) contradicted his earlier observations, saying that the male pleopod 1 is absent.

Callianopsis de Saint Laurent, 1973

Callianopsis de Saint Laurent, 1973: 515.—Schweitzer Hopkins and Feldmann, 1997: 237–238.—Sakai, 2005b: 226.—Sakai, 2011: 478–479.—Dworschak and Poore, 2018: 67.

Pleurocalliax Sakai, 2011: 480–481 (type species, *Callianassa caecigena* Alcock and Anderson, 1894, by original designation and monotypy).

Neocallianopsis Sakai, 2011: 482 (type species, *Callianopsis anovalis* Lin, Komai and Chan, 2007, by original designation and monotypy).

Phaetoncalliax Sakai, Türkay, Beuck and Freiwald, 2015: 124–128 (type species, *Phaetoncalliax mauritana* Sakai, Türkay, Beuck and Freiwald, 2015, by original designation and monotypy).

Type species. Callianassa goniophthalma Rathbun, 1902, by original designation and monotypy.

Diagnosis. ***Rostrum acute, produced, with dorsal carina leading to gastric region***; carapace with median carina strong on rostrum, weaker more posteriorly; cardiac sulci absent. Pleomere 6 with lateral projections. Maxilliped 3 exopod absent. Male major cheliped merus with straight or weakly convex blade on lower margin bearing a short proximal curved spine and 1 or more distal spines.

Remarks. Callianopsis is recognised by the combination of a dorsally carinate rostrum and lateral projections on pleomere 6.

Callianopsis was placed in its own subfamily of the Ctenochelidae by Manning and Felder (1991). The subfamily was included as a member of Gourretiidae by Sakai (2005b) and at family rank by Sakai (2011). Sakai (2005b: 227) treated *Dawsonius*, a gourretiid genus, as a junior synonym of *Callianopsis* but in a note added in proof to the same paper (p. 245) recognised it as a separate genus. Dworschak and Poore (2018) synonymised *Neocallianopsis* Sakai, 2011, *Pleurocalliax* Sakai, 2011, and *Phaetoncalliax* Sakai, Türkay, Beuck and Freiwald, 2015, with *Callianopsis*. All had been inadequately diagnosed or based on errors.

Vulcanocalliax Dworschak and Cunha, 2007

Vulcanocalliax Dworschak and Cunha, 2007: 37.—Sakai, 2011: 350–351.

Type species. Vulcanocalliax arutyunovi Dworschak and Cunha, 2007, by original designation and monotypy.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea; carapace without median carina; cardiac sulci absent. Pleomere 6 without lateral projections. Maxilliped 3 exopod absent. ***Male major cheliped merus with 1–2 small proximal teeth on lower margin***.

Remarks. The sole species, *Vulcanocalliax arutyunovi* Dworschak and Cunha, 2007, was placed in its own subfamily of Callianassidae close to Bathycalliacinae by its authors but the subfamily was transferred to Bathycalliacidae by Sakai (2011). Contrary to Sakai's (2011) assertion, the only species does not have a dorsal plate on the uropodal exopod. It differs from *Bathycalliax geomar* in the absence of cardiac sulci and possession of a maxilliped 3 exopod.

Callichiridae Manning and Felder, 1991

Figures 13–15

Callichirinae Manning and Felder, 1991: 775–776.—Hyžný and Müller, 2012: 968–969.

Calliapaguropinae Sakai, 1999a: 7.—Sakai, 2005: 205.—Sakai, 2011: 491–492.

Callichiridae.—Sakai, 2011: 418.—Sakai et al., 2014: 490 (lapsus, Callichirinae on p. 500).—Dworschak, 2018: 21.

Diagnosis. Rostrum flat, short, triangular, shorter than eyestalks, *or* spike-like, longer than wide; median carina absent; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica oblique in lateral view; ***anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle***; posterior margin of carapace without lateral lobes; pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea, *or* cylindrical, with terminal subspherical cornea (*Calliapagurops* only). Antennal scaphocerite rudimentary. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. Maxilliped 3 dactylus slender, digitiform,

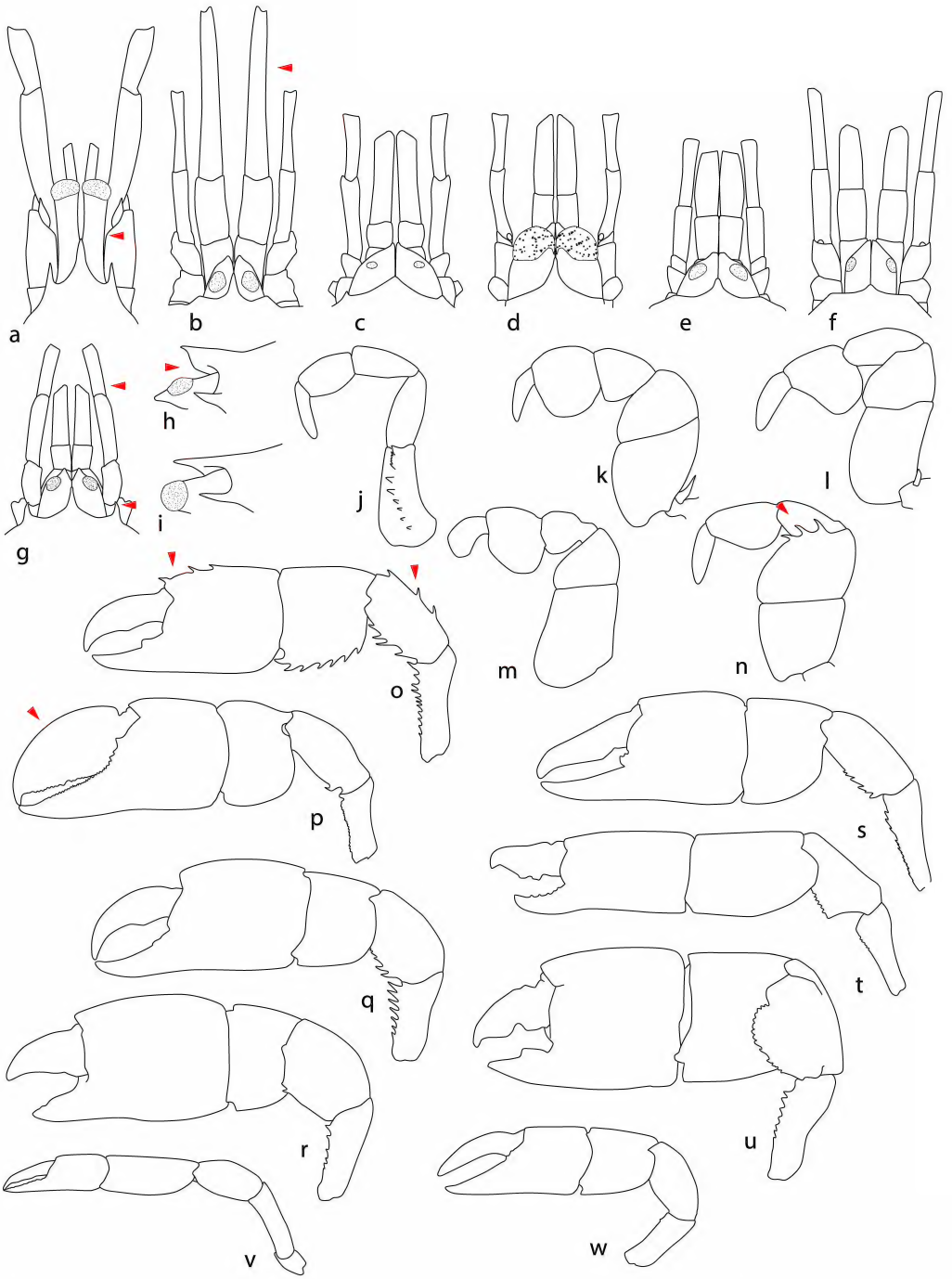

Figure 13. Diagnostic characters for genera of Callichiridae. Rostrum, eyestalks, antennules, antennae: a, *Calliapagurops*; b, *Lepidophthalmus*; c, *Mocallichirus*; d, *Mucrollichirus*; e, *Karumballichirus*; f, *Audacallichirus*; g, h, *Glypturus*; i, *Corallianassa*. Maxilliped 3: j, *Mocallichirus*; k, *Glypturoides*; l, *Karumballichirus*; m, *Thailandcallichirus*; n, *Calliapagurops*. Male major pereopod 1: o, *Glypturus*; p, *Thailandcallichirus*; q, *Corallianassa*; r, *Mucrollichirus*; s, *Karumballichirus*; t, *Glypturoides*; u, *Laticallichirus*. Minor pereopod 1: v, *Balsscallichirus*; w, *Laticallichirus*.

Original illustrations: c, *Mocallichirus mocambiquensis*, UF 13986; d, r, *Mucrollichirus mucronatus*, MNHN-IU-2013-2777.

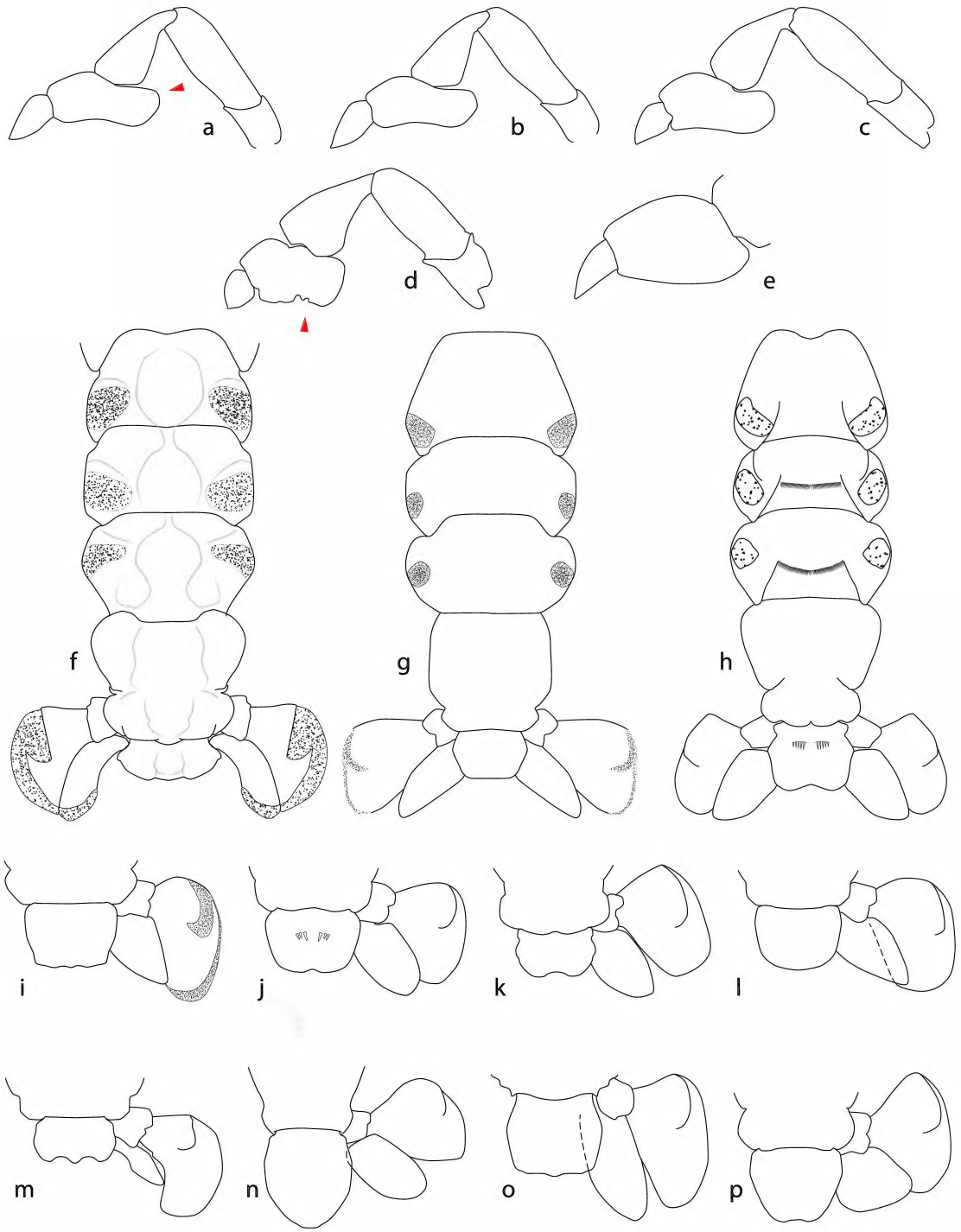

Figure 14. Diagnostic characters for genera of Callichiridae. Pereopod 3: a, *Audacallichirus*; b, *Karumballichirus*; c, *Neocallichirus*; d, *Lepidophthalmus*; e, *Mucrollichirus*. Pleon, telson, uropods: f, *Callichirus*; g, *Grynaminna*; h, *Michaelcallianassa*. Telson, uropod: i, *Audacallichirus*; j, *Balsscallichirus*; k, *Glypturoides*; l, *Karumballichirus*; m, *Lepidophthalmus*; n, *Mocallichirus*; o, *Kraussillichirus*; p, *Neocallichirus*.

Original illustrations: n, *Mocallichirus mocambiquensis*, UF 13986; e, *Mucrollichirus mucronatus*, MNHN-IU-2013-2777.

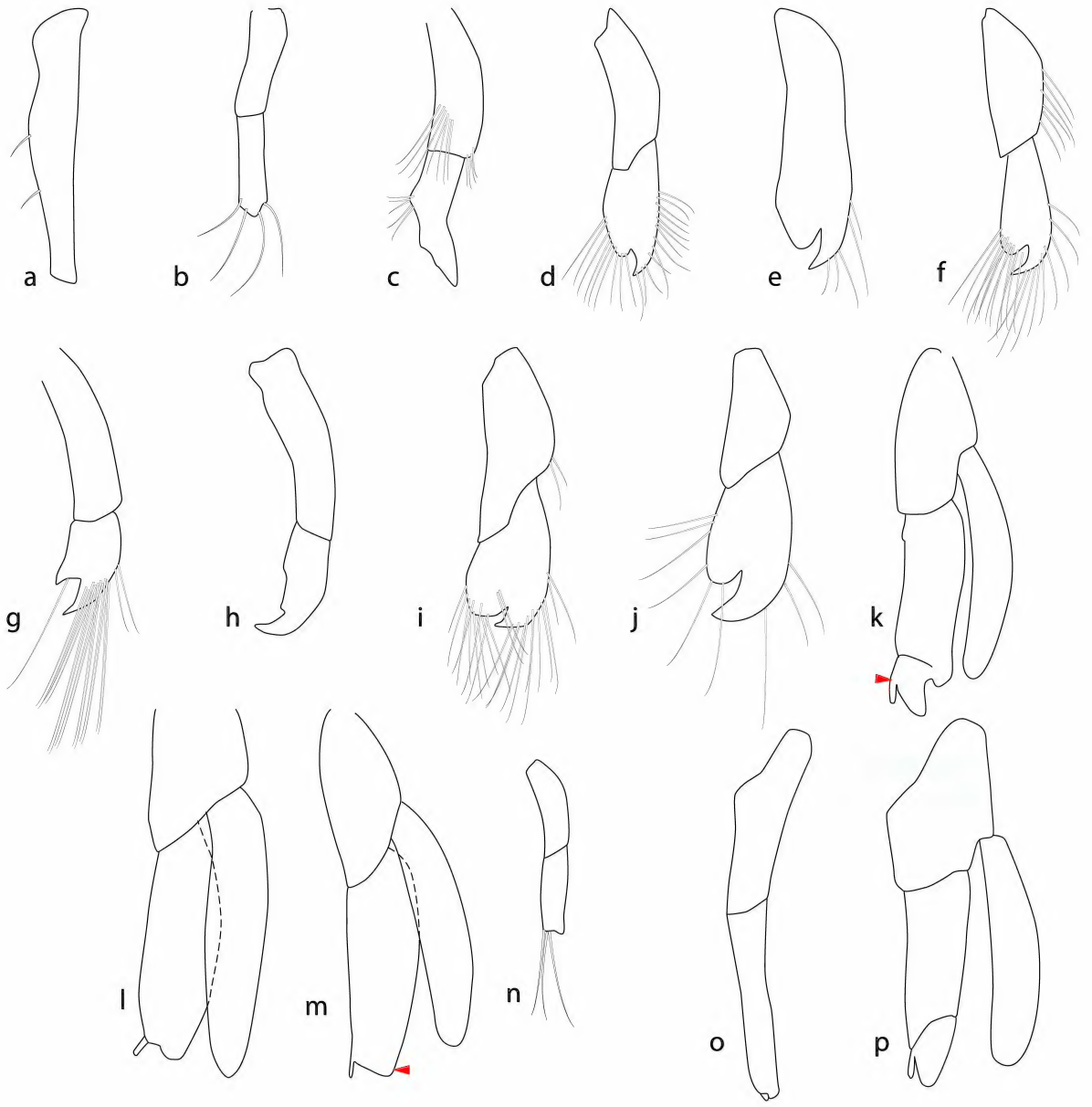

Figure 15. Diagnostic characters for genera of Callichiridae. Male pleopod 1: a, *Mocallichirus mocambiquensis*; b, *Balsscallichirus balssi*; c, *B. pixii*; d, *Corallianassa martensi*; e, *C. xutha*; f, *Glypturus armatus*; g, *Lepidophthalmus eiseni*; h, *L. madagassus*; i, *Neocallichirus raymanningi*; j, *N. vigilax*. Male pleopod 2: k, *Glypturus armatus*; l, *Corallianassa coutierei*; m, *Grynaminna tamakii*; n, *Michaelcallianassa indica*. Female pleopod 2: o, *Balsscallichirus balssi*; p, *Laticallichirus grandis*.

Original illustrations: a, *Mocallichirus mocambiquensis*, UF 13986; j, *Neocallichirus vigilax* MNHN-IU-2015-7072.

with setae irregularly spaced along all margins. Cheliped merus lower margin smooth or spinose; major cheliped with distinctively flattened palm, sometimes with strong crest above and below. Pereopod 3 propodus broad, with proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate or subchelate. Female pleopod 2 rami narrower and with more reduced setation than pleopods 3–5; ***endopod flattened and 2–5 times as long as wide***. Pleopods 3–5 with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae reduced and almost embedded in mesial margin of endopod. Uropodal exopod with elevated dorsal plate.

Remarks. In callichirids, the endopod of the female pleopod 2 is flattened, variously broadened and more or less parallel-sided, unlike in callianassids where it is narrow. The anterior branchiostegal margin is interrupted by an oblique sclerotised ridge, sometimes almost articulating on the margin, unlike in callianassids where this margin is uninterrupted. Pleopod 1 is always present in the male, often substantial with a distolateral sharp curved lobe (fig. 15d–j) or variously reduced (fig. 15a–c), whereas in callianassids it is small and simple or absent. The epipod of maxilliped 1 takes the plesiomorphic form with a triangular lobe overlapping the exopod; this lobe does not exist in callianassids.

The use of the name as a family, rather than subfamily, has not been previously argued.

Key to genera of Callichiridae

1. Eyestalk cylindrical, separate, with terminal spherical cornea, without terminal lobe (fig. 13a); maxilliped 3 merus with 3 spines along distal margin (fig. 13n) ..... *Calliapagurops*

– Eyestalk flattened, contiguous, about twice as long as wide, with cornea subterminal and more or less elevated, with terminal lobe (figs 13b–g); maxilliped 3 merus without spines along distal margin (figs 13j–m) 2

2. Rostrum spine-like, anteriorly or upwardly directed; anterolateral margins of carapace with conical curved spine, sometimes weakly calcified at base (fig. 13g) 3

– Rostrum obsolete or triangular, flat even if sharp; anterolateral margins of carapace not produced (figs 13b–f) or rarely sharp (in *Neocallichirus vigilax*, *Lepidophthalmus tridentatus*) 4

3. Major chelipeds with 3 spines on upper inner margin of merus and propodus, and 4–6 on lower margin of carpus (fig. 13o); rostrum with midventral ridge (fig. 13h); scaphocerite small, discoid; male pleopod 2 with partially articulating appendix masculina (fig. 15k) ..... *Glypturus*

– Major chelipeds without spines on upper margin of merus and propodus or lower margin of carpus (fig. 13q); rostrum without midventral ridge (fig. 13i); scaphocerite absent; male pleopod 2 with appendix masculina fused to endopod (fig. 15l) ..... *Corallianassa*

4. Maxilliped 3 exopod present, minute (figs 13k, l) 5

– Maxilliped 3 exopod absent 8

5. Antennular peduncle much longer than antennal peduncle (fig. 13b); telson posterior margin with medial lobe (fig. 14m, o) 6

– Antennular peduncle shorter than antennal peduncle (fig. 13e); telson posterior margin convex or concave 7

6. Male major cheliped merus with sinuous lower margin, widest proximally and excavate beyond, *or* with proximal tubercle bearing spine(s) with or without more distal teeth along lower margin; pereopod 3 propodus lower margin with obtuse notch between distal lobe and heel (fig. 14d); ..... *Lepidophthalmus*

– Male major cheliped merus with denticulate blade, more prominent over proximal half of lower margin; pereopod 3 propodus lower margin simply concave ..... *Kraussillichirus*

7. Male major cheliped fingers longer than square palm (fig. 13s); telson widest proximally or at midpoint, with convex posterior margin (fig. 14l) ..... *Karumballichirus*

– Male major cheliped fingers shorter than rectangular palm (fig. 13t); telson widest at midpoint, posterior margin concave (fig. 14k) ..... *Glypturoides*

8. Antennular peduncle shorter or as long as antennal peduncle (figs 13c, d, f) 9

– Antennular peduncle significantly longer than antennal peduncle (fig. 13b) 13

9. Major cheliped merus lower margin with simple proximal hook, dactylus massive (fig. 13p); maxilliped 3 dactylus with expanded setose apex (fig. 13m) ..... *Thailandcallichirus*

– Major cheliped merus lower margin denticulate or with toothed blade, dactylus not significantly broadened (figs 13q, r); maxilliped 3 dactylus tapering 10

10. Rostrum spine-like, thickened; cornea subdistal, hemispherical, elevated, with minute mesiodistal plate; female pleopod 2 endopod 3 times as long as wide ..... *Mucrollichirus*

– Rostrum flat, triangular; reaching cornea mid-distal, scarcely elevated, with obvious mesiodistal plate; female pleopod 2 endopod 4 times as long as wide 11

11. Telson parallel-sided over most of length, with obtuse angled apex, domed dorsally (fig. 14n); maxilliped 3 propodus longer than wide, free distal margin oblique; male pleopod 1 consisting of 1 slender article (fig. 15a) ..... *Mocallichirus*

– Telson widest proximally or at midpoint; maxilliped 3 propodus as long as wide, free distal margin nearly transverse; male pleopod 1 consisting of 2 articles 12

12. Telson converging over most of length from subproximal width to about half maximum width, with rounded posterolateral corners, narrow posterior margin (fig. 14p); pereopod 3 propodus with proximal lobe on lower margin slightly overlapping carpus (fig. 14c) ..... *Neocallichirus*

– Telson converging from subproximal width to about three-quarters maximum width, with strongly convex lateral margins and rounded distolateral corners, wide sinuous posterior margin (fig. 14i); pereopod 3 propodus with prominent proximal lobe on lower margin appearing to overlap carpus (fig. 14a) ..... *Audacallichirus*

13. Uropodal endopod strap-like, curved, longer than exopod; pleomeres 3–5 with dorsal pattern of symmetrical grooves; telson almost semicircular, thickened, with constriction on proximal region, with posterolateral swellings (fig. 14f) ..... *Callichirus*

– Uropodal endopod ovate; pleomeres 3–5 without pattern of symmetrical grooves; telson convex-sided, widest proximally or near midpoint (figs 14g, h) 14

14. Uropodal exopod about as wide as length of anterior margin; distal margin of telson convex, upper surface with long setae only (fig. 14g) ..... *Grynaminna*

– Uropodal exopod much wider than length of anterior margin; distal margin of telson concave, upper surface usually with transverse row of short spiniform setae (figs 14h, j) 15

15. Minor cheliped palm about one third as wide as major cheliped palm, carpus longer than wide, fingers straight, shorter than palm (fig. 13v) ..... *Balsscallichirus*

– Minor cheliped palm at least half as wide as major cheliped palm, carpus as long as wide, fingers curved, pincer-like, much longer than palm (figs 13u, w) 16

16. Pleomeres 3–5 with anteriorly converging longitudinal grooves and oblique–transverse rows of long setae (fig. 14h); male major cheliped merus with lower margin almost straight; female pleopod 2 uniramous (fig. 15o) ..... *Michaelcallianassa*

– Pleomeres 3–5 with prominent lateral tufts of setae; male major cheliped merus with convex denticulate blade (fig. 13u); female pleopod 2 biramous (fig. 15p) ..... *Laticallichirus*

Implicit attributes. Unless indicated otherwise, the following attributes are implicit throughout the generic diagnoses. Rostrum without midventral ridge; anterolateral spines absent, anterolateral angle obsolete. Pleomere 1 tergite and oblique narrow lateral pleura fused into a single sclerifed unit, *or* pleura separated by triangular uncalcified region from tergite; rectangular median lateral sternite plates (pleopod attached) fused to pleuron and median sternite. Pleomeres 3–5 without symmetrical pattern of deep grooves, with narrow transverse rows of setae, pleomere 6 without longitudinal grooves on anterior section, with slight lateral incision. Eyestalk flattened and contiguous. Antennular peduncle length less than 3 times as width of both eyestalks, shorter than antennal peduncle. Antennal scaphocerite vestigial. Maxilliped 3 merus without distal spine on mesial margin; crista dentata a row of numerous denticles; propodus longer than wide, lower margin convex; dactylus tapering, with scattered setae over upper margin, dense brush of short setae distally on lower margin; exopod absent. Male major cheliped carpus shorter than palm; without spines on upper margin of merus and propodus or lower margin of carpus; male major cheliped dactylus typically tapering. Pereopod 3 propodus lower margin straight or weakly concave. Male pleopod 2 biramous. Female pleopod 2 biramous; endopod about 4 times as long as wide. Telson smooth dorsally.

Audacallichirus gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:F54AD76A-8172-4D0F-ADCB-2174D5A3FC6B

Type species. Callianassa audax De Man, 1911, by present designation.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse ridge. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; ***propodus about as wide as long***, free distal margin transverse or nearly so. Male major cheliped merus lower margin convex or blade like, especially proximally, with small denticles. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, ***article 2 distally expanded, with shallow apical notch between 2 rounded setose distal lobes***. Male pleopod 2 appendix interna absent or reduced to obsolete distomesial lobe. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson convex-sided, widest near midpoint, posterior margin trilobed, excavate each side of medial lobe.

Etymology. An alliteration of the name of the type species and *Callichirus*, type genus of the family.

Remarks. Audacallichirus audax differs from members of *Neocallichirus*, the genus in which it was placed by Sakai (1999a, 2011), in having a telson with strongly convex lateral margins, uropodal endopod tapering, the propodus of pereopod 3 usually with a strong proximal lobe on the lower margin, and the male pleopod 1 with a broad second article with an wide apical notch (Ngoc-Ho, 2014; Rao and Kartha, 1967; Tirmizi, 1967). The molecular analysis of Robles et al. (in press) found the species similar to *Neocallichirus mirim*, a species sometimes included in *Sergio*. The two species share a similar male pleopod 1, uropodal endopod, telson and cheliped, but the propodus of pereopod 3 is less expanded in *N. mirim*.

Balsscallichirus Sakai, 2011

Balsscallichirus Sakai, 2011: 414–415.—Hyžný, 2016: 43–46.

Tirmizicallichirus Sakai, 2011: 474–475 (type species, *Callianassa* (*Callichirus*) *masoomi* Tirmizi, 1970, by original designation and monotypy).

Barnardcallichirus Sakai, 2011: 416–417 (type species, *Callichirus tenuimanus* de Saint Laurent and Le Loeuff, 1979, by original designation).

Capecalliax Sakai, 2011: 345 (type species, *Callianassa pixii* Kensley, 1976, by original designation and monotypy) **syn. nov.**

Forestcallichirus Sakai, 2011: 426–427 (type species, *Callichirus foresti* Le Loeuff and Intès, 1974, by original designation and monotypy) **syn. nov.**

Type species. *Callianassa* (*Callichirus*) *balssi* Monod, 1933, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite divided into 2 sections by unsclerified band; tergite weakly sclerotised, if so only posteriorly; pleura oblique thin rods independent of tergite dorsally, separated by extensive flexible region; sternite a thin transverse plate. Antennular peduncle longer than antennal peduncle. ***Maxilliped 3 ischium and merus narrow, at least 3 times as long as wide at their articulation***; crista dentata absent (or few proximal spines only); propodus longer than wide, lower margin convex or about as wide as long, free distal margin clearly oblique or free distal margin transverse or nearly so. Male major cheliped merus with lower margin almost straight or with denticulate blade, more prominent over proximal half of lower margin or with prominent proximal denticulate blade-like tooth on lower margin. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave, lower margin straight or weakly concave or weakly convex. Pereopod 4 subchelate. Male pleopod 1 of 2 articles, article 2 longer than wide, with or without slight apical notch. Male pleopod 2 biramous or uniramous; ***appendix interna absent***. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners or with convex lateral margins and rounded posterolateral corners, posterior margin trilobed, excavate each side of medial lobe or slightly excavate or obscurely excavate between rounded posterolateral corners, with transverse row of robust setae.

Remarks. *Balsscallichirus* is best recognised by its very narrow maxilliped 3. Sakai (2011) distinguished *Balsscallichirus* (*B. balssi*, *B. guineensis*), *Tirmizicallichirus* (*T. masoomi*), *Barnardcallichirus* (*B. tenuimanus, B. gilchristi*) and *Forestcallichirus* (*F. foresti*) from *Podocallichirus* (*P. madagassus*) on the basis of male pleopods 1 and 2. The distinction is valid—*Podocallichirus* is considered here a junior synonym of *Lepidophthalmus*. He did not compare the new genera with each other or with others. Hyžný (2016) synonymised *Tirmizicallichirus* and *Barnardcallichirus* with *Balsscallichirus* and listed five Recent species and four fossils.

Kensley (1976) recognised that his new species *Callianassa pixii* belonged in the "subgenus *Callichirus*", likening it to *Callianassa guineensis*. He was supported by de Saint Laurent and Le Loeuff (1979), who grouped this with four of the species listed above, *B. balssi, B. foresti, B. tenuimanus* and *B. guineensis* (as species of *Callianassa*), on the similarity of triangular rostrum, rounded posterior border of the telson, pediform maxilliped 3 and reduced male pleopod 2. Sakai (2011) erected another monotypic genus, *Capecalliax* for *C. pixii*, this time in the family Anacalliacidae, to which it clearly does not belong. *Capecalliax* and *Forestcallichirus*, for *C. foresti* listed in this group correctly characterised by de Saint Laurent and Le Loeuff (1979) are also synonyms of *Balsscallichirus*. The exceptionally narrow maxilliped 3 was treated as a symplesiomorphy by the morphological analysis of Robles et al. (in press).

The seven species are known only from around Africa, as far north as Mauritania in the west and Pakistan in the east.

Calliapagurops de Saint Laurent, 1973

Calliapagurops de Saint Laurent, 1973: 515.—Sakai, 1999a: 8.—Ngoc-Ho, 2002: 540–541.—Sakai, 2005b: 207.—Sakai, 2011: 492.

Type species. *Calliapagurops charcoti* de Saint Laurent, 1973, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum spine-like; anterolateral spines prominent. Pleomere 1 tergite undivided or with weak transverse ridge. ***Eyestalk cylindrical, with subspherical terminal pigmented cornea***. Antennal scaphocerite elongate, longer than wide, with free acute tip. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation; merus with 2 or more distal spines on distal free margin; crista dentata of few separate spines proximally and toothed ridge distally overlapping proximal margin of merus; propodus about as wide as long, free distal margin clearly oblique. Male major cheliped merus with row of sharp oblique spines, usually 2 proximally and 1 or more along length of lower margin. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus oval, lower margin convex, not proximally lobed (slightly produced distally), lower margin weakly convex. Pereopod 4 propodus minutely chelate, fixed finger as long as dactylus. Male pleopod 1 consisting of 2 articles, article 2 longer than wide, with or without slight apical notch. Male pleopod 2 appendix interna free, articulating, distal on mesial endopodal margin. Female pleopod 2 endopod 2–3 times as long as wide. Pleopods 3–5 appendices internae barely emerging from endopodal margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson convex-sided, widest near midpoint, posterior

margin concave between rounded posterolateral corners, with transverse row of robust setae.

Remarks. The two species of *Calliapagurops* differ from all other callianassoids in having cylindrical eyestalks with terminal cornea. Ngoc-Ho (2002) pointed out numerous similarities between *Calliapagurops* and *Corallianassa*, similarities borne out in the morphological analysis (Robles et al., in press) but not by the molecular data, where the genus is closer to *Grynaminna*. Sakai (2011) argued that *Calliapagurops* and its subfamily Calliapaguropinae belong in Eucalliacidae because of differences from *Callichirus* and Callichirinae, namely the absence of the dorsal oval, the unique eyestalks and a small appendix interna on the male pleopod 2. He listed no similarities to Eucalliacidae – there are few.

Callichirus Stimpson, 1866

Callichirus Stimpson, 1866: 47.—de Saint Laurent and Le Loeuff, 1979: 55–56.—Manning and Felder, 1991: 775–776.—Sakai, 2011: 418 (abbreviated synonymy).

Callianassa (*Callichirus*).—Borradaile, 1903: 546–547.—De Man, 1928: 28, 96 (partim).

Type species. *Callianassa major* Say, 1818, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite divided into 2 sections by unsclerified band; tergite weakly sclerotised, if so only posteriorly; pleura oblique thin rods independent of tergite dorsally, separated by extensive flexible region; sternite a thin transverse plate. ***Pleomeres 3–5 with symmetrical pattern of deep curved transverse and longitudinal grooves plus paired tufts of dense setae, pleomere 6 with pair of deep longitudinal grooves on wide swollen anterior section, defined by lateral concavity.*** Antennular peduncle length longer than antennal peduncle. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation; crista dentata absent (or few proximal spines only); propodus about as wide as long, free distal margin clearly oblique or free distal margin transverse or nearly so. Male major cheliped merus with denticulate blade, more prominent over proximal half of lower margin or with prominent proximal denticulate blade-like tooth on lower margin; major cheliped carpus much longer than palm, especially in male. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 longer than wide, with or without slight apical notch. Male pleopod 2 appendix interna absent or reduced to obsolete distomesial lobe. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod strap-like, posterior margin concave. Telson thickened, with constriction on anterior region, with posterolateral swellings, posterior margin with medial notch at end of longitudinal groove.

Remarks. Species of *Callichirus* are recognised by the symmetrical pattern of deep curved transverse and longitudinal grooves plus paired tufts of dense setae on pleomeres 3–5, deep longitudinal grooves on the wide anterior section of pleomere 6, the long antennular peduncle, the strap-like curved uropodal endopods and the thickened telson, with a proximal constriction. *Callichirus kraussi* is here removed to its own genus, *Kraussillichirus*, on genetic evidence (Robles et al., in press) and uropodal endopods more typical of the family. Species of *Callichirus* may be functional hermaphrodites with some or all females having male gonopores (Souza et al., 2017, 2018)

Corallianassa Manning, 1987

Corallianassa Manning, 1987: 392–394.—Poore, 2004: 184.—Ngoc-Ho, 2005: 71.—Komai et al., 2015: 54–55 (synonymy).

Corallichirus Manning, 1992: 571–574.—Sakai, 2011: 422–423 (type species: *Corallianassa xutha* Manning, 1988, by original designation).

Type species. *Callianassa longiventris* A. Milne-Edwards, 1870, by original designation.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. ***Rostrum spine-like***; ***anterolateral spines prominent***. Pleomere 1 tergite undivided or with weak transverse ridge. Maxilliped 3 ischium and merus linear, around twice as long as wide at their articulation; crista dentata of few separate spines proximally and toothed ridge distally overlapping proximal margin of merus; propodus about as wide as long, free distal margin transverse or nearly so. Male major cheliped merus with row of sharp oblique spines, usually 2 proximally and 1 or more along length of lower margin. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave, lower margin straight or weakly concave or weakly convex. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna free, articulating, distal on mesial endopod margin. Pleopods 3–5 appendices internae longer than wide, clearly emerging from margin of endopod. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. ***Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners***, posterior margin straight or with slight medial lobe.

Remarks. Corallianassa is best recognised by the prominent anterolateral spines, the hemispherical, elevated, distal cornea (distinguishing it from *Calliapagurops*) and the absence of marginal teeth on the chelipeds (distinguishing it from *Glypturus*; see Komai et al., 2015). Komai et al. (2015) reviewed the complex taxonomic history of *Corallianassa*, *Corallichirus* and *Glypturus*, and the unjustified confusion introduced by Sakai's (2011) revival of *Corallichirus*, regarded as a synonym of *Corallianassa* since this was first proposed by Ngoc-Ho (2005).

Glypturoides Sakai, 2011

Glypturoides Sakai, 2011: 428.

Type species. Callianassa trilobata Biffar, 1970, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse ridge. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation; propodus about as wide as long, ***free distal margin transverse or nearly so***; ***exopod present***. Male major cheliped merus lower margin convex or blade like, especially proximally, with small denticles. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave or weakly convex. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna absent or reduced to obsolete distomesial lobe. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson with convex lateral margins and rounded posterolateral corners, ***posterior margin concave between rounded posterolateral corners***.

Remarks. Glypturoides trilobata, the only species, is like species of *Neocallichirus* but with an exopod on maxilliped 3. In addition, the maxilliped 3 propodus has the free distal margin more oblique than in typical *Neocallichirus*, and the telson is short with convex lateral margins and concave posterior margin.

Glypturus Stimpson, 1866

Glypturus Stimpson, 1866: 46.—Manning, 1987: 390.—Manning and Felder, 1991: 778.—Sakai, 1999a: 72.—Sakai, 2005b: 130–132.—Sakai, 2011: 429–430 (partim).—Hyžný and Müller, 2012: 969–971.—Hyžný et al., 2013: 133.—Klompmaker et al., 2015: 11.—Komai et al., 2015: 53–54 (complete synonymy).

Callianassa (*Glypturus*).—Borradaile, 1903: 548.

Type species. Glypturus acanthochirus Stimpson, 1866: 46, by original designation.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum spine-like, with midventral ridge; anterolateral spines prominent. Pleomere 1 tergite fused, divided into 2 sections by transverse groove or shoulder. Antennal scaphocerite small, discoid. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; crista dentata of few separate spines proximally and toothed ridge distally overlapping proximal margin of merus; propodus about as wide as long, free distal margin transverse or nearly so. ***Major cheliped merus with row of sharp oblique spines, usually 2 proximally and 1 or more along length of lower margin***; ***with 3 spines on upper inner margin of merus and propodus, and 4–6 on lower margin of carpus.*** Minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna free, articulating, distal on mesial endopod margin. Pleopods 3–5 appendices internae longer than wide, clearly emerging from margin of endopod. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. ***Telson strongly diverging to beyond midpoint and semicircular distally***, posterior margin broadly semicircular.

Remarks. Glypturus is best recognised by the prominent anterolateral spines and the presence of marginal teeth on the chelipeds (Komai et al., 2015). Komai et al. (2015) clarified the confusion around *Glypturus* introduced by Sakai's (2011) revision.

Grynaminna Poore, 2000

Grynaminna Poore, 2000: 150–151.—Sakai, 2011: 438–439.—Hyžný and Karasawa, 2012: 63–65.

Type species. Grynaminna tamakii Poore, 2000, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse ridge. Antennular peduncle length more than 3 times the width of both eyestalks, longer than antennal peduncle. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; crista dentata consisting of a row of numerous denticles; propodus about as wide as long, free distal margin transverse or nearly so. ***Male major cheliped merus with convex tuberculate blade on most of lower margin***. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 propodus minutely chelate, fixed finger as long as dactylus. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna free, articulating, distal on mesial endopod margin (fig. 15m). Pleopods 3–5 appendices internae barely emerging from endopodal margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide.

Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners, posterior margin straight or convex between tapering posterolateral margins.

Remarks. Only one Recent species is known. The antennular peduncle is particularly long, the rostrum particularly short and the merus of the major cheliped has a convex tuberculate blade along most of its lower margin.

Karumballichirus gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:E21E0313-3989-4E03-BBB6-9F9844028DC0

Type species. Callianassa karumba Poore and Griffin, 1979, by present designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum spine-like. Pleomere 1 tergite fused, divided into 2 sections by transverse groove or shoulder. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; propodus about as wide as long, free distal margin clearly oblique; ***exopod present***. ***Male major cheliped merus lower margin straight, irregularly dentate, usually with 1 more prominent proximal denticulate tooth***. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave or weakly convex. Pereopod 4 propodus simple, distally rounded on lower margin. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna free, articulating, distal on mesial endopodal margin. Pleopods 3–5 appendices internae barely emerging from endopodal margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson with convex lateral margins and rounded posterolateral corners, posterior margin straight or convex between tapering posterolateral margins.

Etymology. An alliteration of the name of the type species and *Callichirus*, type genus of the family.

Remarks. Karumballichirus differs from the most similar callichirid genera, *Neocallichirus*, in which it was most recently placed (see Sakai, 1988) and *Corallianassa* (see Komai et al., 2015) in possession of a short maxillipedal 3 exopod, a feature shared with *Lepidophthalmus*, which is its sister taxon on the molecular phylogram (Robles et al., in press). The type species was described in detail by Dworschak (2008). The type species was recognised as the extant representative of a group of similar fossil species by Hyžný et al. (2017).

Kraussillichirus gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:07353B50-6C2E-4CD3-A3DF-F37D1497A8C3

Type species. Callianassa kraussi Stebbing, 1900, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite divided into 2 sections by unsclerified band; tergite weakly sclerotised, if so only posteriorly; pleura oblique thin rods independent of tergite dorsally, separated by extensive flexible region; sternite a thin transverse plate. ***Antennular peduncle length more than 3 times the width of both eyestalks***, longer than antennal peduncle. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation; crista dentata absent (or few proximal spines only); propodus about as wide as long, free distal margin transverse or nearly so; ***exopod present***. Male major cheliped merus with denticulate blade, more prominent over proximal half of lower margin. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave or weakly convex. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 longer than wide, with or without slight apical notch. ***Male pleopod 2 appendix interna absent***. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson with convex lateral margins and rounded posterolateral corners, posterior margin convex, with medial lobe.

Etymology. An alliteration of the name of the type species and *Callichirus*, type genus of the family.

Remarks. Callianassa kraussi was included in the subgenus *Callichirus* by De Man (1928) and the genus *Callichirus* by Sakai (2005b and later). *Kraussillichirus* resembles *Callichirus* but differs in lacking its ornamented pleomeres 3–6 and having an ovoid uropodal endopod (fig. 14o). The only species appears to be estuarine (Hanekom and Russell, 2015; Siebert and Branch, 2005) as are species of *Lepidophthalmus*, which it also somewhat resembles.

Laticallichirus Komai, Yokooka, Henmi and Itani, 2019

Laticallichirus Komai et al., 2019: 463–466.

Type species. "Neocallichirus" grandis Karasawa and Goda, 1996, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. ***Rostrum spine-like***. Pleomere 1 tergite divided into 2 sections by unsclerotised band; tergite weakly sclerotised, if so only posteriorly; pleura oblique thin rods independent of tergite

dorsally, separated by extensive flexible region; sternite a thin transverse plate. Antennular peduncle length more than 3 times the width of both eyestalks, longer than antennal peduncle. Maxilliped 3 ischium and merus broad, less than twice as long as wide at their articulation; crista dentata absent; propodus about as wide as long, free distal margin clearly oblique. Male major cheliped merus with convex denticulate blade. Male minor cheliped much narrower than major, carpus longer than palm, fingers shorter than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 of 2 articles, article 2 longer than wide, with or without slight apical notch. ***Male pleopod 2 appendix interna absent***. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson with convex lateral margins and rounded posterolateral corners, posterior margin concave between rounded posterolateral corners, with transverse row of robust setae.

Remarks. The type species was described from Japanese Middle Pleistocene fossil chelipeds but extant specimens enabled the species to be described more completely. Komai et al. (2019) compared the new genus with several others. Their phylogram based on the 16S rRNA gene found the species closest to *Callichirus* and more remote from a clade including *Neocallichirus*, *Corallianassa*, *Glypturus*, *Glypturoides* and *Lepidophthalmus*. The genus appears closest to *Michaelcallianassa*, as our key indicates.

Lepidophthalmus Holmes, 1904

Lepidophthalmus Holmes, 1904: 310.—Manning and Felder, 1991: 778–779.—Sakai, 1999a: 64–65.—Sakai and Apel, 2002: 278.—Sakai, 2005b: 143–144.—Felder, 2001: 440.—Sakai, 2011: 446.—Robles and Felder, 2015: 462–464, 467–468, fig. 1.—Komai et al., 2018: 23–24.

Podocallichirus Sakai, 1999a: 53–54.—Sakai, 2005b: 187–189 (partim).—Sakai, 2011: 466–467.—Hyžný and Muñiz, 2012: 619–621.—Hyžný and Karasawa, 2012: 62–63.—Hyžný, 2016: 44–45.—Komai et al., 2018: 24 (type species: *Callianassa madagassa* Lenz and Richters, 1881, by original designation and monotypy) **syn. nov.**

Lepidophthalmoides Sakai, 2011: 440–441 (type species: *Lepidophthalmus eiseni* Holmes, 1904, by original designation) **objective synonym.**

Lepidophthalminus Sakai, 2015: 433 (replacement name for *Lepidophthalmus* sensu Sakai, 2011; type species, *Callianassa bocourti* A. Milne-Edwards, 1870, by original designation) **syn. nov.**

Type species. *Lepidophthalmus eiseni* Holmes, 1904, by monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge which it meets level with linea thalassinica. Rostrum spine-like; anterolateral angles obsolete or spinous. Pleomere 1 tergite undivided or with weak transverse step. Antennular peduncle length less than 3 times as width of both eyestalks or more than 3 times the width of both eyestalks (rare), longer than antennal peduncle. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation, *or* rarely less than twice as long as wide at their articulation; crista dentata absent (or few proximal spines only); propodus about as wide as long, free distal margin clearly oblique, *or* free distal margin transverse or nearly so; ***dactylus curved, 3 times as long as wide, concave below***; ***exopod present***. Male major cheliped merus with sinuous lower margin, widest proximally and excavate beyond, *or* with proximal tubercle bearing spine(s) with or without more distal teeth along lower margin; dactylus typically tapering, *or* massive, upper margin expanded, strongly convex, dentate. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave, lower margin with broad deep notch between distal lobe and heel. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 tapering, with small acute subdistal lobe, acute distal apex. Male pleopod 2 appendix interna absent, *or* reduced to obsolete distomesial lobe, *or* apparent only as field of hooks on side of appendix masculina. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson with convex lateral margins and rounded posterolateral corners, ***posterior margin trilobed, excavate each side of medial lobe, or convex, with medial lobe***.

Remarks. *Lepidophthalmus* differs from other callichirids in the combination of short antennal peduncle, telson with convex lateral margins and quasi-trilobed posterior margin, a series of concavities along the lower margin of the propodus of pereopod 3, and a curved narrow dactylus on maxilliped 3. Some species have particularly setose fingers on the minor cheliped or with long setae on the mesial face of the major cheliped extending into the gape between the fingers. *Lepidophthalmus* shares an exopod on maxilliped 3 with *Karumballichirus*, *Kraussillichirus* and *Glypturoides*.

Sakai (2011) placed eight species in his new genus *Lepidophthalmoides* Sakai, 2011, an objective synonym of *Lepidophthalmus* Holmes, 1904. Both have the same type species. Sakai (2015) realised the error and erected *Lepidophthalminus* Sakai, 2015, to replace *Lepidophthalmus* sensu Sakai, 2011, this time with *Callianassa bocourti* A. Milne-Edwards, 1870, as type species, with only five included species and referring to his 2011 diagnosis of *Lepidophthalmus* to differentiate it from *Lepidophthalmus* Holmes, 1904. Sakai (2011) separated the two "genera" in the male pleopod 1 being "chelate" in the former and simple in the latter. Incidentally, the adjective "chelate" is inappropriate in this context—the second article has a mesiodistal notch, not formed by two distal opposing articles. A review of all 15 known species reveals that one pleopod form grades into the other and may reflect developmental stages. Komai et al. (2018) has already pointed out that the generic division of Sakai (2015) has no merit. *Lepidophthalminus* is here synonymised with *Lepidophthalmus*.

No consistent morphological difference was found between American and Indo-West Pacific species (Komai et al., 2018;

Robles et al., in press; Robles and Felder, 2015). Most species of *Lepidophthalmus* are found in estuarine habitats where their ecology has been studied (Felder, 2001; Filho et al., 2013; Hernáez et al., 2012).

Michaelcallianassa Sakai, 2002

Michaelcallianassa Sakai, 2002: 480–481.—Sakai, 2005b: 156–157.—Sakai, 2011: 450.

Type species. *Michaelcallianassa indica* Sakai, 2002, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. ***Pleomeres 3–5 with anteriorly converging longitudinal grooves and oblique-transverse rows of long setae***. Antennular peduncle longer than antennal peduncle. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; propodus about as wide as long, free distal margin clearly oblique. ***Male major cheliped merus with lower margin almost straight***. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 of 2 articles, article 2 longer than wide, with or without slight apical notch. ***Male pleopod 2 uniramous***; appendix interna absent or reduced to obsolete distomesial lobe. ***Female pleopod 2 uniramous***. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners, posterior margin concave between rounded posterolateral corners, with transverse row of robust setae.

Remarks. The two species of *Michaelcallianassa* have uniramous pleopods 2 in both sexes distinguishing the genus from all other callichirids (fig. 15n). The telson has a transverse row of robust setae. Sakai (2002) noted that the type species was similar to species of *Callichirus* but has a row of setae between the two dorsolateral tufts on pleomeres 4 and 5. This row is not present on the second species, *M. sinica* (see Liu and Liu, 2009).

Mocallichirus gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:8E845452-37C7-4271-B787-E28D6285AE8F

Type species. *Callianassa mocambiquensis* Sakai, 2004, by present designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; crista dentata a row of numerous denticles; propodus free distal margin clearly oblique. Male major cheliped merus with denticulate blade, more prominent over proximal half of lower margin. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 propodus simple, distally rounded on lower margin. ***Male pleopod 1 consisting only of 1 article***. Male pleopod 2 uniramous; appendix interna absent or reduced to obsolete distomesial lobe. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson parallel-sided over most of length, with broadly rounded apex, domed, posterior margin broadly semicircular.

Etymology. An alliteration of the name of the type species and *Callichirus*, type genus of the family.

Remarks. Robles et al.'s (in press) molecular analysis placed *Callianassa mocambiquensis* sister to *Michaelcallianassa* (two species) in Callichiridae. Sakai (2004) thought the species similar to *Callianassa plantei* Sakai, 2004 (also found in Mozambique), *C. joculatrix* and three others, all members of Callianassidae s.s. GCBP was able to examine numerous specimens from Madagascar from the collections of MNHN and FMNH. The broad female pleopod 2 , the attenuated distal lobe on the epipod of maxilliped 1 and the apical notch on the male pleopod 1 confirm the species as a callichirid. The species is recognisable by the unusual shape of the telson; it is domed, longer than in most callichirids with a broadly semicircular posterior half parallel-sided over most of length, with broadly rounded apex. The antennal peduncle is longer than the antennular peduncle, the male pleopod 1 is of one article and the male pleopod 2 uniramous.

Mocallichirus mocambiquensis shares with members of the callianassid genus *Coriollianassa* a proximal neck on the carpus of the chelipeds, a case of remarkable convergence.

Mucrollichirus gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:B57E69B6-D096-459C-B4AF-0D278A73B557

Type species. *Callianassa mucronata* Strahl, 1862, by present designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. ***Rostrum spine-like***. Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; propodus about as wide as long, free distal margin

clearly oblique. Male major cheliped merus lower margin convex, *or* blade like, especially proximally, with small denticles. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. ***Pereopod 3 propodus oval, lower margin convex, not proximally lobed***. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna absent or reduced to obsolete distomesial lobe. Female pleopod 2 endopod 2–3 times as long as wide. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners, posterior margin straight or with slight medial lobe, smooth dorsally.

Etymology. An alliteration of the name of the type species and *Callichirus*, type genus of the family.

Remarks. Mucrollichirus has a more weakly lobed propodus on pereopod 3 than all other genera except *Calliapagurops*. The new genus differs from *Neocallichirus* (see Sakai, 1988), *Corallianassa* (see Komai et al., 2015) and other similar genera in having a shorter telson. Both the morphological and molecular analyses placed *Mucrollichirus mucronatus* on a clade sister to *Corallianassa* (Robles et al., in press). The similarity to *Neocallichirus*, the genus in which the species was most recently placed (Sakai, 2011), is more remote.

The molecular analysis of Robles et al. (in press) found no difference between individuals from Papua New Guinea and the Philippines but illustrations of *Mucrollichirus mucronatus* vary (De Man, 1888, 1928; Dworschak, 1992; Poore and Griffin, 1979; Sakai, 1999a; Sakai et al., 2014; Tirmizi, 1977).

Neocallichirus Sakai, 1988

Neocallichirus Sakai, 1988: 61–62.—Manning and Felder, 1991: 779–780.—Poore, 1994: 102.—Sakai, 1999a: 84–86.—Sakai, 2000: 92.—Davie, 2002: 461.—Poore, 2004: 184.—Sakai, 2005b: 160–162.—Sakai, 2011: 451–452.—Hyžný and Karasawa, 2012: 60–65.

Sergio Manning and Lemaitre, 1994: 40.—Sakai, 2011: 467–468 (type species, *Callianassa guassutinga* Rodrigues, 1971, by original designation).—Hyžný and Karasawa, 2012: 61–62.

Callichiropsis Sakai, 2010: 1453 (type species, *Callichiropsis spiridonovi* Sakai, 2010, by original designation and monotypy) **syn. nov.**

Type species. Neocallichirus horneri Sakai, 1988, by original designation.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge with which it articulates by means of a virtual condyle. Rostrum obsolete or obtusely triangular, flat, not reaching cornea; anterolateral spines absent (rarely with small spines). Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 ischium and merus linear; propodus about as wide as long, free distal margin transverse or nearly so. Male major cheliped merus lower margin convex or blade like, especially proximally, with small denticles. Male minor cheliped palm half or more width of major cheliped palm, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 ovoid, with shallow apical notch between rounded subdistal lobe and curved acute apex. Male pleopod 2 appendix interna reduced to obsolete distomesial lobe, *or* rarely free, articulating, distal on mesial endopod margin, *or* absent. Pleopods 3–5 appendices internae barely emerging from endopod margin. ***Uropodal endopod with straight or slightly convex anterior margin ending in rounded angle, transverse or near-transverse distal margin continuous with curved posterior margin, as wide or wider than long***. Telson converging to about half basal width from near anterior width over most of length to rounded posterolateral corners, posterior margin straight or with slight medial lobe.

Remarks. Neocallichirus is the largest callichirid genus. The uropodal endopod has a straight or slightly convex anterior margin ending in a rounded angle and continuous distal and posterior margins. The endopod is often wider than long. The telson tapers regularly to about half its width. Sakai (2011) provided a key to 28 species, including *N. mucronatus*, herein removed to *Mucrollichirus* gen. nov., and *N. karumba* (=*N. kempi*), herein removed to *Karumballichirus* gen. nov. Sakai (1999a, 2005b) included *Sergio* in the synonymy of *Neocallichirus*, but in 2011 he redefined the former and placed some of its originally included species in a re-diagnosed genus. He differentiated *Sergio* with a notched apex on the male pleopod 1 (adult form) from *Neocallichirus* with only a slight distal indentation (juvenile form), despite most species of *Neocallichirus* being described as having the adult form. The molecular analysis (Robles et al., in press) placed three species of "*Sergio*" within the *Neocallichirus* clade, a result anticipated by Sepahvand et al. (2018).

Sakai (2010) differentiated a new genus *Callichiropsis* from *Lepidophthalmus* on the basis of a different pereopod 3 and from *Podocallichirus* on the shape of the telson. We treat *Podocallichirus* as a synonym of *Lepidophthalmus* (see above). He did not compare *Callichiropsis spiridonovi* Sakai, 2010, with *Neocallichirus*, from which it does not differ. *Callichiropsis* is here synonymised with *Neocallichirus*.

Thailandcallichirus Sakai, 2011

Thailandcallichirus Sakai, 2011: 473–474.—Komai et al., 2018: 23–24.

Type species. Callianassa ranongensis Sakai, 1983, by original designation and monotypy.

Diagnosis. Anterior branchiostegal lobe sclerotised, well produced anteriorly beyond junction with oblique branchiostegal ridge, which it meets level with linea thalassinica. Rostrum spine-like. Pleomere 1 tergite undivided or with weak transverse step. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; crista dentata absent (or few proximal spines only); propodus about as wide as long, free

distal margin clearly oblique; ***dactylus curved, about twice as long as wide, concave below***. Male major cheliped merus with proximal tubercle bearing spine(s) with or without more distal teeth along lower margin; ***dactylus massive, upper margin expanded, strongly convex, smooth***. Male minor cheliped half or more as wide as major, carpus as long as or shorter than palm, fingers as long as or longer than palm. Pereopod 3 propodus subpentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin straight-concave, lower margin with broad deep notch between distal lobe and heel. Pereopod 4 subchelate. Male pleopod 1 consisting of 2 articles, article 2 tapering, with small acute subdistal lobe and acute distal apex. Male pleopod 2 appendix interna absent or reduced to obsolete distomesial lobe. Pleopods 3–5 appendices internae barely emerging from endopod margin. Uropodal endopod with convex anterior margin, acute-rounded apex, straight-slightly curved posterior margin, longer than wide. Telson tapering from greatest width near base, posterior margin straight or convex between tapering posterolateral margins.

Remarks. Thailandcallichirus differs from *Lepidophthalmus*, its closest sibling, in having the antennular peduncle shorter than the antennal, rather than the other way around, a more compact maxilliped 3 dactylus, lacking a maxillipedal 3 exopod, a convex posterior margin on the telson and in having a massive dactylus on the major cheliped (Komai et al., 2018). The minor cheliped is distally setose as in some *Lepidophthalmus* species. Sakai (2011) justified his new genus on differences between the type species and *Neocallichirus*, the genus in which he had previously placed it (Sakai, 1999a, 2005b). Tudge et al. (2000) found it was a sister to other species of *Lepidophthalmus* and treated it as a species of this genus as did Robles and Felder (2015). Robles et al. (in press) found this alliance again but had no molecular data to support it.

Ctenochelidae Manning and Felder, 1991

Figures 16, 17

Ctenochelinae Manning and Felder, 1991: 784.—Poore, 1994: 103.—Sakai, 1999c: 87.—Sakai, 2005b: 235.

Gourretiinae Sakai, 1999c: 95.—Sakai, 2017a: 1124.

Gourretiidae.—Sakai, 2004: 556.—Sakai, 2005b: 217.—Sakai, 2011: 507–508.—Sakai, 2017a: 1124–1125.—Dworschak and Poore, 2018: 68.

Ctenochelidae.—Sakai, 2005b: 235.—Sakai, 2011: 485–486.—Dworschak et al., 2012: 189–190.—Poore and Dworschak, 2017: 122 (synonymy).

Pseudogourretiinae Sakai, 2005b: 230.

Dawsoniinae Sakai, 2006: 1276–1277.—Sakai, 2011: 507.—Sakai, 2017a: 1124.

Ctenocheloidae (pro Ctenocheloididae) Sakai, 2011: 595–596.—Poore, 2015b: 142 **syn. nov.**

Pseudogourretiidae Sakai, 2011: 507–508, 523.

Tosacallianassidae Sakai, 2016: 813.

Diagnosis. Rostrum spike-like, longer than wide; median carina absent, *or* rarely on rostrum only; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica horizontal or oblique in lateral view; anterior branchiostegal margin sinusoidal or semicircular, *or* with deep obtuse notch leading to oblique ridge; ***anterior branchiostegal lobe simple, scarcely calcified, merging smoothly with anterodorsal branchiostegal angle and anterolateral margin of carapace***; posterior margin of carapace without lateral lobes. Pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite simple, triangular. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. Maxilliped 3 propodus longer than wide, not prominently lobed on lower margin; dactylus slender, digitiform, with setae irregularly spaced along all margins. Cheliped merus lower margin smooth or with prominent proximal tooth; major cheliped with cylindrical palm, fingers elongate and pectinate, or with distinctively flattened palm, sometimes with strong crest above and below. Pereopod 3 propodus rectangular or oval, up to twice as long as wide, with proximal lobe on lower margin, without distal spiniform setae on lateral face or lower margin. ***Pereopod 5 semichelate (fixed finger closing on proximal part of dactylus), dactylus a twisted plate longer than finger.*** Female pleopod 2 rami narrower and with more reduced setation than pleopods 3–5; endopod flattened and 2–3 times as long as wide. Pleopods 3–5 with oblique peduncles, endopods oval, exopods attached laterally, not proximally lobed, shorter than and barely overlapping endopods, *or* with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae elongate, much longer than wide. Uropodal exopod without elevated dorsal plate, *or* with margin divided by notch.

Remarks. Robles et al. (in press) found Ctenochelidae to have strong molecular support and two morphological synapomorphies. The character states shared by members of this family are maxilliped 3 with a prominent toothed crista dentata, usually extending beyond the meral distal margin, and a semichelate pereopod 5, its dactylus a twisted plate longer than the finger. Two clades, ctenochelids s.s. and gourretiids, were supported by morphological characters but not by molecular relationships.

Manning and Felder (1991) treated Ctenochelidae as one of two "callianassid-like families", distinguished from Callianassidae by the presence of an appendix masculina on the male pleopod 2, which was incorrect, as realised later by Felder and Manning (1994: 352), a longitudinally carinate uropodal exopod, lacking a dorsal plate and a carapace usually with a cardiac prominence. Their arrangement was followed by Poore (1994). The genera of Ctenochelidae known to these authors are treated in three families here. Sakai (1999c) included only *Paracalliax* beside the type genus and excluded *Dawsonius* and *Gourretia* in a new subfamily Gourretiinae. Sakai (2005b) elevated the taxon to family rank, retaining its single subfamily that he ignored in Sakai (2011), and confined Ctenochelidae to *Ctenocheles*.

As pointed out by Poore (2015b), Sakai's (2011) diagnosis of his new family Ctenocheloididae (as Ctenocheloidae) is virtually the same as Anker's (2010) diagnosis of *Ctenocheloides* and was

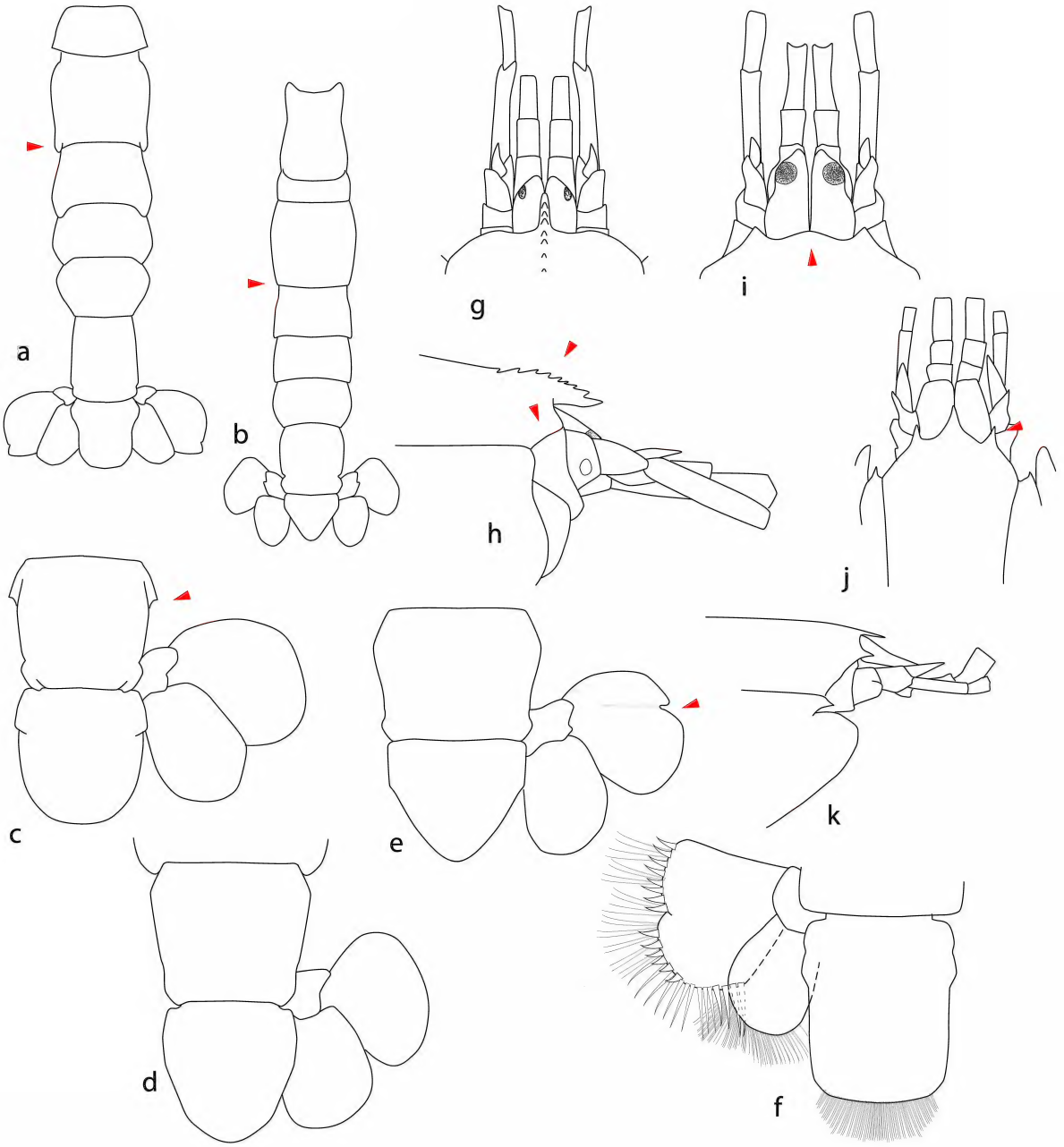

Figure 16. Diagnostic characters for genera of Ctenochelidae. Pleon (suture between pleomeres 2 and 3 indicated): a, *Ctenocheles*; b, *Ctenocheloides*. Pleomere 6, telson, uropod: c, *Dawsonius*; d, *Gourretia*; e, *Paragourretia*; f, *Laurentgourretia*. Rostrum, eyestalks, antennules, antennae: g, h, *Ctenocheles*; i, *Ctenocheloides*; j, k, *Laurentgourretia*.

Original illustrations: f, j, k, *Laurentgourretia rhopalommata*, MNHN-IU-2014-11417.

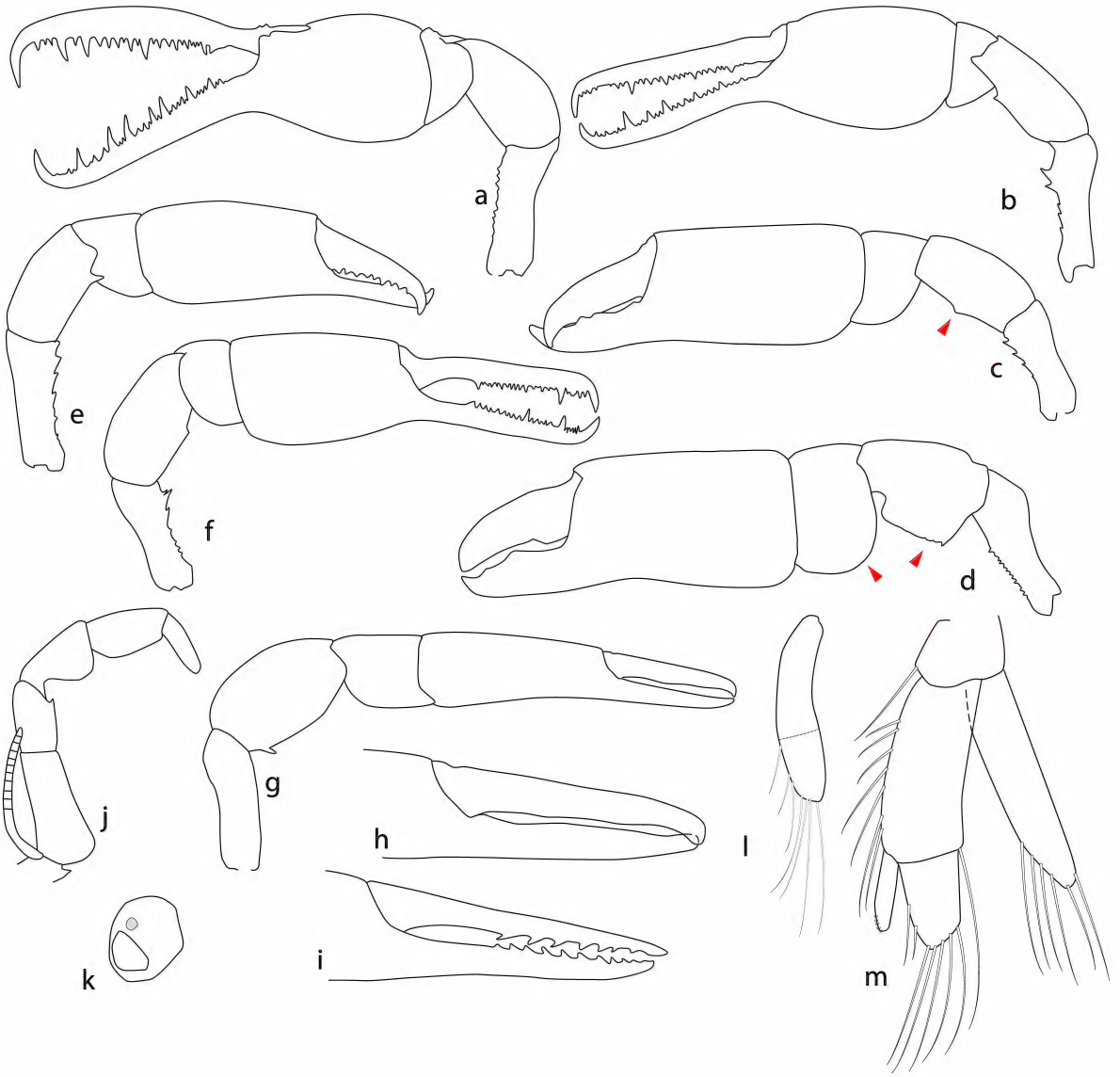

Figure 17. Diagnostic characters for genera of Ctenochelidae. Major cheliped: a, *Ctenocheles*; b, *Ctenocheloides*; c, *Kiictenocheloides*; d, *Gourretia*. Minor cheliped: e, *Ctenocheloides*; f, *Kiictenocheloides*; g, h, *Paragourretia*; i, *Gourretia*. Maxilliped 3: j, *Gourretia*. Male coxa 5: k, *Laurentgourretia*. Male pleopods 1, 2: l, m, *Laurentgourretia*.

Original illustrations: k–m, *Laurentgourretia rhopalommata*, MNHN-IU-2014-11417.

presented without a strong argument for why family status is to be preferred over genus status for its single species. We treat Ctenocheloididae as a junior synonym. Poore and Dworschak (2017) synonymised three taxa erected by Sakai and Türkay (2016), Tosacallianassidae with Ctenochelidae, *Tosacallianassa* with *Ctenocheles*, and *T. hatasagaensis* with *Ctenocheles balssi*.

Gourretiinae was established by Sakai (1999c) as a subfamily of Callianassidae for *Gourretia* de Saint Laurent, 1973, and *Dawsonius* Manning and Felder, 1991. Sakai (2004) elevated the taxon to family level and added *Callianopsis* de Saint Laurent, 1973, and two new genera, *Laurentgourretia* and *Paragourretia*. Pseudogourretiinae was then added for another new genus, *Pseudogourretia* Sakai, 2005b. Sakai (2006) recognised Callianopsinae and Pseudogourretiinae as subfamilies of Gourretiidae and added Dawsoniinae for *Dawsonius*. All subfamilies were ignored in Sakai's (2011) synthesis where four of the genera discussed earlier were included; *Paracalliax* was added although it had earlier been treated as member of its own family (see discussion under Paracalliacidae below), and *Callianopsis* was excluded (see Callianopsidae discussed above).

Sakai (2017b) radically dissected Gourretiidae, introducing five new genera. *Paragourretia* and *Dawsonius* were treated as synonyms of *Gourretia*, *Paracalliax* was retained and his earlier genus *Pseudogourretia* ignored. Justification of the new genera centred on differences between the male pleopods 1 and 2. He stressed the significance of these sexually differentiated structures, citing their importance in the taxonomy of other decapods and their greater significance than the few cheliped characters available to palaeontologists (Hyžný and Klompmaker, 2015). However, he took no account of pleopodal developmental as individuals mature from juveniles to adults. All five of Sakai's (2017b) new genera are herein synonymised with either *Gourretia* or *Paragourretia*.

On strictly cladistic criteria, *Dawsonius* is a senior synonym of *Paragourretia* on molecular evidence (Robles et al., in press). But the genus has unique apomorphies apparent in the morphological treatment, pleomere 6 with triangular lateral projections, maxilliped 3 exopod absent and pereopod 3 with a triangular propodus proximally produced on the lower margin. Otherwise the two genera have the same uropods, male pleopods and chelipeds.

Pseudogourretia, said by Sakai (2005b) to possess pleurobranchs, was found by Dworschak and Poore (2018) to not have pleurobranchs, as all callianassoids, and the genus was synonymised with *Gourretia*. The only character placing the sole species, *P. portsudanensis* in *Gourretia* rather than *Paragourretia* is the oval pereopod 3 propodus; chelipeds and uropods are missing from the only specimen. The family erected for it (Sakai, 2011) likewise is a junior synonym of Ctenochelidae.

Key to genera of Ctenochelidae

1. Major cheliped with palm swollen, with narrow pectinate fingers longer than palm (figs 17a, b) 2
– Major cheliped with palm flattened, upper and lower margins usually ridged, fingers rarely longer than palm (figs 17c, d) 3
2. Rostrum spine-like, dorsally carinate; cornea flat, with weak pigmentation (fig. 16g); pleomeres 1 and 2 together half as long as pleomeres 3–5 (fig. 16a) ..... *Ctenocheles*
– Rostrum obsolete, flat; cornea disc-like, strongly pigmented (fig. 16i); pleomeres 1 and 2 together as long as pleomeres 3–5 (fig. 16b) ..... *Ctenocheloides*
3. Telson longer than wide, parallel-sided over most of length, with curved truncate apex (fig. 16f); carapace with anterolateral spines (figs 16j, k); maxilliped 3 exopod absent ..... *Laurentgourretia*
– Telson shorter or longer than wide, tapering over most of length to rounded apex (figs 16c–e); anterolateral angles of carapace obsolete; maxilliped 3 exopod present (fig. 17j) or absent 4
4. Pleomere 6 with triangular lateral projections (fig. 16c); telson broadly rounded over posterior two-thirds (fig. 16c) ..... *Dawsonius*
– Pleomere 6 without triangular lateral projections (*P. biffari* excepted); telson tapering over posterior half to two-thirds (figs 16d, e) 5
5. Major cheliped merus lower margin with tubercle at midpoint (fig. 17c); minor cheliped palm swollen, fingers pectinate, spines erect (fig. 17f); maxilliped 3 exopod absent ..... *Kiictenocheloides*
– Major cheliped merus lower margin with straight or weakly convex blade on lower margin bearing a short proximal curved spine and 1 or more distal spines (fig. 17d); minor cheliped palm tapering (fig. 17g), fingers with or without teeth; maxilliped 3 exopod present (fig. 17j) 6
6. Minor cheliped with sharp proximally directed teeth along cutting edges of fingers (fig. 17i); major cheliped carpus lower proximal margin swollen (fig. 17d); uropodal exopod without marginal notch (fig. 16d) ..... *Gourretia*
– Minor cheliped without sharp teeth along cutting edges of fingers (figs 17g, h); major cheliped carpus lower proximal margin tapering; uropodal exopod usually with marginal notch, slight dorsal plate (fig. 16e) ..... *Paragourretia*

Implicit attributes. Unless indicated otherwise, the following attributes are implicit throughout the generic diagnoses. Cardiac prominence absent. Anterolateral angle obsolete, unarmed. Pleomere 6 without lateral projections. Maxilliped 3 merus with 1 mesiodistal spine; exopod absent. Major cheliped carpus proximal and lower margins oblique, evenly curved; propodus rectangular, fingers stout, fixed finger with broad tooth. Minor cheliped merus lower margin smooth.

Ctenocheles Kishinouye, 1926

Ctenocheles Kishinouye, 1926: 36.—de Saint Laurent, 1973: 514.—Poore and Griffin, 1979: 277.—de Saint Laurent and Le Loeuff, 1979: 81–83.—Sakai, 1999c: 88.—Sakai, 2005b: 237–238.—Sakai, 2011: 486–487 (key to species).—Hyžný et al., 2014: 249–250.—Poore and Dworschak, 2017: 122 (synonymy).

Tosacallianassa Sakai and Türkay, 2016: 813 (type species,

Tosacallianassa hatasagaensis Sakai and Türkay, 2016, by original designation and monotypy).

Type species. *Ctenocheles balssi* Kishinouye, 1926, by monotypy.

Diagnosis. Cardiac prominence present. ***Rostrum blade-like, produced anteriorly***. Male major cheliped merus with oblique spine near midpoint of lower margin (or absent); propodus swollen, with fine pectinate fingers at least twice as long as palm. Minor cheliped merus lower margin smooth, *or* with spine at or near midpoint; propodus cylindrical, slightly swollen at midpoint, about twice as wide as long. Male pleopod 1 article 2 simple, tapering, without coupling hooks. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. The blade-like rostrum combined with the fine long pectinate fingers of the major cheliped of *Ctenocheles* make its species easily recognisable. In fact, some species are known only from these claws (Holthuis, 1967; de Saint Laurent, 1979a). To the six described species listed by Sakai (2005b, 2011) can be added *C. plantei* (Burukovsky, 2005), described as a member of the lobster genus *Thaumastochelopsis* Bruce, 1988 (Poore and Dworschak, 2017).

Ctenocheloides Anker, 2010

Ctenocheloides Anker, 2010: 1790–1791.—Sakai, 2011: 596.—Poore, 2015b: 142–143.

Type species. *Ctenocheloides attenboroughi* Anker, 2010, by original designation and monotypy.

Diagnosis. ***Cardiac prominence present***. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. ***Maxilliped 3 merus with mesial spine at midpoint***. Male major cheliped merus with oblique spine near midpoint of lower margin; propodus swollen, with fine pectinate fingers about as long as palm. Minor cheliped merus lower margin with spine at or near midpoint; propodus cylindrical, slightly swollen at midpoint, about twice as wide as long. Male pleopod 1 article 2 simple, tapering, without coupling hooks. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. The pectinate fingers on the major cheliped are a little longer than the palm, whereas in *Ctenocheles* the fingers are at least twice as long as the palm, and the spikes more pronounced. Three species are known (Poore, 2015b). *Ctenocheloides boucheti* is a sister taxon to two species of *Ctenocheles* in the molecular analysis (Robles et al., in press).

Dawsonius Manning and Felder, 1991

Dawsonius Manning and Felder, 1991: 785.—Sakai, 2005b: 245.—Sakai, 2011: 508.

Gourretia.—Sakai, 2017a: 1128–1129 (partim).

Type species. *Callianassa latispina* Dawson, 1967, by original designation and monotypy.

Diagnosis. Cardiac prominence present. Rostrum sharply triangular, produced to near apex of ocular lobes. ***Pleomere 6 with lateral projections***. Male major cheliped merus with straight or weakly convex blade on lower margin bearing a short proximal curved spine and 1 or more distal spines; propodus rectangular, fingers fine, fixed finger smooth. Minor cheliped merus lower margin with erect proximal spine (as in major cheliped); propodus tapering, about 3 times as long as wide, with long narrow fingers. Pereopod 3 propodus triangular, with straight upper margin, expanded proximally on lower margin. Male pleopod 1 article 2 with lobed distomesial margin, distal notch, sharp curved distolateral apex. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. *Dawsonius latispina* differs from other ctenochelids (except *Paragourretia biffari* Blanco Rambla and Liñero Arana, 1994) in having lateral projections on pleomere 6.

Manning and Felder (1991) differentiated *Dawsonius* from *Gourretia* on the absence of an exopod on maxilliped 3 and the sharp lateral projections on pleomere 6. We (DLF) can confirm that maxillipedal 3 exopod is absent (Dawson, 1967; Manning and Felder, 1991) and that Biffar's (1971a) figure and Sakai's (2011) observation of an exopod are in error. Biffar's figures are a composite from types and Honduran material but the latter is *P. biffari*.

Sakai (2005b) treated the genus first as a synonym of *Callianopsis* and in an addendum as a separate genus that he differentiated from *Callianopsis*. *Callianopsis* is a member of another family. He did not explain what he meant by "sensu Sakai (not Manning and Felder, 1991)" before his new diagnosis. Sakai (2011) included *Dawsonius* in Gourretiidae. Sakai's (2011) observations of a "paratype" and a "lectotype" (USNM 103755, 172310) were not made on the holotype and paratype designated by Dawson (1967); these specimens may well have been misidentified. Sakai's (2011: fig. 69E) figure of the apex of the male pleopod 2 is impossible to reconcile with Manning and Felder (1991: fig. 16i), which is typical of the family, nor with any ctenochelid.

Sakai (2017a) synonymised *Dawsonius* with *Gourretia* on the basis of the same male pleopods 1 and 2. In fact, *Dawsonius* is unique in pleopod 1 possessing a distomesial rounded blade and acute apex, whereas in *Gourretia* and *Paragourretia* the distomesial lobed is acute and smaller than the apical lobe.

Gourretia de Saint Laurent, 1973

Gourretia de Saint Laurent, 1973: 514.—Le Loeuff and Intès, 1974: 26.—Poore and Griffin, 1979: 278.—Manning and Felder, 1991: 785.—Sakai, 2002: 468–469.—Ngoc-Ho, 2003: 498–499.—Sakai, 2005b: 218–219 (partim).—Sakai, 2011: 510–511 (partim).

Pseudogourretia Sakai, 2005b: 230–231.—Dworschak and Poore, 2018: 68–70 (type species, *Pseudogourretia portsudanensis* Sakai, 2005, by original designation and monotypy).

Ivorygourretia Sakai, 2017a: 1126, 1130 (type species, *Gourretia barracuda* Le Loeuff & Intès, 1974, by original designation and monotypy) **syn. nov.**

Plantesgourretia Sakai, 2017a: 1126, 1131 (type species, *Gourretia nosybeensis* Sakai, 2004, by original designation and monotypy) **syn. nov.**

Ruiyuliugourretia Sakai, 2017a: 1126, 1131–1133 (type species, *Gourretia sinica* Liu and Liu, 2010, by original designation and monotypy) **syn. nov.**

Type species. *Callianassa subterranea* var. *minor* Gourret, 1887, by original designation and monotypy (now *Gourretia denticulata* Lutze, 1937 [Lewinsohn and Holthuis, 1986]).

Diagnosis. Rostrum sharply triangular, produced to near apex of ocular lobes, *or* obsolete, *or* obtusely triangular, flat, not reaching cornea (rarely). ***Maxilliped 3 with exopod***. Male major cheliped merus with straight or weakly convex blade on lower margin bearing a short proximal curved spine and 1 or more distal spines; ***carpus proximal and lower margins convex, swollen; propodus broad, with short fingers***. Minor cheliped merus lower margin with erect proximal spine (as in major cheliped); propodus tapering, about 3 times as long as wide; fingers ***evenly tapering, straight, dactylus longer, with sharp spines along opposing edges***. Pereopod 3 propodus oval, little longer than wide, with short rounded proximal lobe on lower margin, lower margin straight, upper margin strongly convex. Male pleopod 1 article 2 with sharp distomesial apex, distal notch, sharp curved distolateral apex. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. In species of *Gourretia* the minor cheliped propodus tapers evenly, the fingers are straight, the dactylus being slightly longer, and both fingers have sharp spines, almost hook-like in some, along their opposing edges. The fixed finger of the major cheliped is stout, as is the dactylus, and blade-like with a broad tooth. The fused appendices on the male pleopod 2 reach or overlap the end of the endopod. This contrasts with the minor chelipeds of species of *Paragourretia* whose fingers lack the sharp spines and curve distally, the fixed finger of the major cheliped evenly tapers and curves, and the appendices on the male pleopod 2 are midmesial, far from the apex of the endopod.

Sakai (2004) separated *Paragourretia* from *Gourretia* for two species (see discussion below). In Sakai (2011), the two genera were redefined and four additional species were reallocated to *Paragourretia* from *Gourretia*. The key character indicated then to separate the two genera was said to be the absence in *Gourretia* and presence in *Paragourretia* of a "lateral notch" on the uropodal exopod. A cardiac prominence is absent in the former but present in the latter according to their diagnoses. The presence or absence of a distal notch is sometimes difficult to judge—it is not a black and white character (see comments below under *Paragourretia*). Our morphological analysis separates *Paragourretia* from *Gourretia* on the structure of the major and minor chelipeds, the shape of the propodus of pereopod 3 and the position of the appendices on the male pleopod 2, the notch being of lesser importance. None of these characters was included in the generic diagnoses by Sakai (2005b, 2011). The allocation of known species between the two genera is the same as that of Sakai (2011).

Pseudogourretia was synonymised with *Gourretia* by Dworschak and Poore (2018).

The male pleopod 1 of *G. barracuda* (Le Loeuff and Intès, 1974), said by Sakai (2017a) to be "hooked distally", ends in a simple apex, a more subdued form of the bifid apex usual in this genus. The pleopod may be a subadult form. The appendix masculina of the male pleopod 2 is more adpressed to the endopod apex than typical but the basic structure is the same. *Ivorygourretia*, erected for only this species, is here synonymised with *Gourretia*.

Plantesgourretia Sakai, 2017, erected for only *G. nosybeensis*, was said to have the male pleopod 2 "biramous; exopod shorter than endopod; endopod bilobed distally, and inner lobe bearing distally appendix masculina with setae, but no appendix interna". The exopod is shorter in most species; the appendix masculina is more dominant than in other species but is otherwise similar; we give no importance to the absence of the appendix interna. *G. nosybeensis* is otherwise similar to all species of *Gourretia*; *Plantesgourretia* is here synonymised.

Ruiyuliugourretia Sakai, 2017, again erected for a single species, was said to have special male pleopods 1 and 2. The outline of pleopod 1 is typical of species of *Gourretia* and its supposed four articles are probable artefacts. Pleopod 2 is typical, except for the absence of an appendix interna, as in the previous species. *Ruiyuliugourretia* is here synonymised with *Gourretia*.

Gourretia loeuffintesi Sakai, 2005, is a nomen nudum (no holotype designated).

Kiictenocheloides Sakai, 2013

Kiictenocheloides Sakai, 2013: 1693.

Type species. *Ctenocheloides nomurai* Komai, 2013, by original designation and monotypy.

Diagnosis. Rostrum obsolete or obtusely triangular, flat, not reaching cornea. Male major cheliped merus with oblique spine near midpoint of lower margin; ***propodus broad, with short fingers***. Minor cheliped merus lower margin with spine at or near midpoint; propodus cylindrical, slightly swollen at midpoint, about twice as wide as long, ***with long narrow fingers***. Male pleopod 1 article 2 simple, tapering, without coupling hooks. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. The swollen propodus and thin pectinate fingers, typical of *Ctenocheles* and *Ctenocheloides* (fig. 17a, b), are not found in *Kiictenocheloides* where the major cheliped has a propodus and fingers (fig. 17c) typical of callianassoids generally. The female pleopods are unknown.

Laurentgourretia Sakai, 2004

Laurentgourretia Sakai, 2004: 557.—Sakai, 2005b: 224.—Sakai, 2011: 515.—Sakai, 2017a: 1126, 1130.

Type species. *Laurentgourretia rhopalommata* Sakai, 2004, by original designation and monotypy.

Diagnosis. Rostrum sharply triangular, produced to near apex of ocular lobes; ***anterolateral spines prominent***. Maxilliped 3 merus with 2 or more mesiodistal spines; exopod absent. Minor cheliped merus lower margin smooth; propodus cylindrical, slightly swollen at midpoint, about twice as wide as long. Male pleopod 1 article 2 simple, tapering, without coupling hooks. Telson mostly parallel-sided, with rounded posterolateral corners.

Remarks. The only species differs from other ctenochelids in the parallel-sided telson (fig. 18h) and having three meral spines on the maxilliped 3. Its chelipeds are unknown.

The only specimen (MNHN-IU-2014-11417) of the type species is a male with male-like pleopods and a gonopore on the coxa of pereopod 5 (figs 17k–m; GCBP observations), not a female as stated by Sakai (2004). The male pleopod 1 has only one weak suture, the second article half as long as the first and with eight marginal setae; the male pleopod 2 is essentially as in other ctenochelids. Its major cheliped is missing. Sakai (2004) diagnosed *Laurentgourretia*, distinguishing it from *Gourretia*, as having a "stick-like" eyestalk, a remarkably sharp scaphocerite, and maxilliped 3 lacking an exopod. The eyestalks are more wedge-shaped in our view (figs 16j, k), contiguous as in other ctenochelids but not as tapering in dorsal view. The scaphocerite is similar to that of *Dawsonius*, which also lacks an exopod on maxilliped 3. The anterolateral angles of the dorsal carapace are sharp, as is the anterodorsal angle of the branchiostegite (fig. 16k). The uropodal exopod has a distal notch as in *Paragourretia* but its margin has stronger marginal spiniform setae (fig. 16f).

The genus is sister to *Dawsonius* in the morphology phylogram; no molecular data are available.

Paragourretia Sakai, 2004

Paragourretia Sakai, 2004: 568–569.—Sakai, 2005b: 225.—Sakai, 2011: 516.

Heterogourretia Sakai, 2017a: 1126, 1129–1130 (type species, *Gourretia aungtonyae* Sakai, 2002, by original designation and monotypy) **syn. nov.**

Tuerkaygourretia Sakai, 2017a: 1126, 1133 (type species, *Tuerkaygourretia galathea* Sakai, 2017, by original designation and monotypy) **syn. nov.**

Type species. *Gourretia phuketensis* Sakai, 2002, by original designation and monotypy.

Diagnosis. Cardiac prominence absent (rarely), *or* present. Rostrum sharply triangular, produced to near apex of ocular lobes, *or* obsolete, *or* obtusely triangular, flat, not reaching cornea. Pleomere 6 without or with (*P. biffari* only) lateral projections. ***Maxilliped 3 with exopod***. Male major cheliped merus with straight or weakly convex blade on lower margin bearing a short proximal curved spine and 1 or more distal spines; propodus rectangular, ***fingers tapering, fine, fixed finger smooth***. Minor cheliped merus lower margin with erect proximal spine (as in major cheliped); propodus tapering, about 3 times as long as wide; fingers ***evenly tapering, curved distally, of equal lengths, smooth or with obscure denticles along opposing edges***. Pereopod 3 propodus linear, longer than wide, without proximal lobe on lower margin, lower margin straight, upper margin moderately convex. Male pleopod 1 article 2 with sharp distomesial apex, distal notch, and sharp curved distolateral apex. Telson parallel-sided over anterior half, then tapering to evenly rounded apex.

Remarks. *Paragourretia* differs from *Gourretia* in having fingers lacking the sharp spines seen in *Gourretia* and curving distally, the fixed finger of the major cheliped evenly tapering and curving, and the appendices on the male pleopod 2 being midmesial, far from the apex of the endopod rather than distal. None of these characters was mentioned by Sakai (2011) although his allocation of species between the two genera is identical to ours. None of the specific diagnoses of members of this genus and of *Gourretia* in Sakai (2011) includes other than an idiosyncratic assemblage of family and generic features and none that tell one species from another. *Paragourretia biffari* shares with *Dawsonius latispina* lateral projections on pleomere 6.

Sakai (2004) likened *Paragourretia* to *Dawsonius*, not *Gourretia*, because of a thick carapace and a cardiac prominence. Re-examination of the type species failed to convince GCBP that the carapace differed from other species of *Gourretia* in this regard. A transverse cardiac sulcus was difficult to decipher, and a transverse row of setae on the anterior branchial region said to also characterise the genus is found in all ctenochelid species examined. Sakai (2011) changed the emphasis of his re-diagnosis, this time relying on the presence of a notch on the uropodal exopod and on simple versus subchelate pereopod 4 (it is simple in both genera). This notch might be a precursor to a "dorsal plate", or as in some species, an elevated anterior margin over the posterior part of the exopod, the two separated by transverse furrow. While the notch is clear and unmissable in some species, in others it is more ambiguous. The notch is a vague concavity in the type species *P. phuketensis* and absent in *P. lahouensis* (which Sakai curiously included in his key to species, identifiable as "without lateral notch"). The notch is absent in all species of *Gourretia*. *Paragourretia* was synonymised with *Gourretia* by Sakai (2017b) because they have similar male pleopods 1 and 2. In fact, in species of *Paragourretia* the appendices on the midmesial margin do not reach the end of the endopod whereas in *Gourretia* s.s. they do, as far as is known.

Gourretia aungtonyae was provisionally included in *Paragourretia* by Sakai (2005b) and made type species of a new genus *Heterogourretia* (Sakai, 2017a) because of the absence of male pleopod 1 and a distal "segmented" appendix interna on pleopod 2. The holotype male has carapace length of 2.9 mm and an ovigerous female 3.6 mm. The small size of the male suggests it is immature and lacks male pleopod 1 for this reason. The figured appendix interna is atypical of axiideans and possibly an artefact. In all other features, the species is typical of *Paragourretia*. For these reasons, *Heterogourretia* is synonymised with *Paragourretia*.

The type species of *Tuerkaygourretia*, *T. galathea* Sakai, 2017, was based on a holotype female from Tranquebar, SE India (*Galathea* stn 290), two paratypes from the same station, two females from the Bay of Bengal, India (*Galathea* stn 304), and one male from Singapore (*Galathea* stn 357). The figures of the holotype (Sakai, 2017a: figs 4A, B, C, E, F, 5A–C, E, G) are of a species of *Paragourretia* showing the minor cheliped without teeth, uropodal exopod with a notch and pereopod 3 with a narrow propodus having the lower margin straight. Other figures are problematic, somewhat undermining Sakai's (2011) argument for new genera based on differences in male pleopods. Fig. 5I of pleopod 2 (said to be from the type locality) and fig. 5D of a broad pereopod 3 (from the Thai-Danish Expedition stn 1160 but not otherwise listed) are of a species of *Gourretia*. Other figures

from the Thai-Danish Expedition stn 1160 are fig. 5H of pleopod 2 of a species of *Gourretia* (appendices terminal) and figs 5J, K of a species of *Paragourretia* (appendices mesial). Sakai (2017a) attributed differences between these two forms to size. It is apparent that more than one species, from both *Gourretia* and *Paragourretia*, have been confounded in this description. Sakai (2017a) did not explain how these pleopodal forms differed from those of other genera. To add further confusion, the species' distribution is given as "Off Tranquebar, India (type locality); W. of Subitana, Port Moresby, Papua New Guinea; West Malay Peninsula; Singapore Island" but material is listed for only the first and last of these four; the Thai-Danish Expedition stn 1160 would appear to be on the West Malay Peninsula. *Tuerkaygourretia* is synonymised with *Paragourretia* on the basis of probable illustrations of the holotype and paratype.

Eucalliacidae Manning and Felder, 1991

Figures 18, 19

Eucalliinae Manning and Felder, 1991: 781 (misspelling).

Eucalliacinae Sakai, 1999a: 108–109.—Ngoc-Ho, 2003: 487–489 (partim).—Sakai, 2005b: 195–196 (partim).—Sakai, 2011: 493–494.—Hyžný, 2012: 51–52.—Sakai, 2017a: 1122.—Sakai, 2018: 734–738.

Eucalliacidae.—Sakai, 2011: 491.—Sakai and Türkay, 2014: 190 (outdated key to genera).—Sakai, 2017a: 1122.—Dworschak, 2018: 17.—Sakai, 2018: 734–738.

Diagnosis. Rostrum flat, short, triangular, shorter than eyestalks; median carina absent; gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica horizontal in lateral view; anterior branchiostegal margin sinusoidal or semicircular; anterior branchiostegal lobe simple, scarcely calcified, merging smoothly with anterodorsal branchiostegal angle and anterolateral margin of carapace; posterior margin of carapace without lateral lobes. Pleomere 1 without anterolateral lobes, weakly chitinised. Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite rudimentary. Maxilla scaphognathite without long seta on posterior lobe extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. ***Maxilliped 3 propodus about as wide as long; dactylus dilating, truncate, with dense field of setae on distal margin. Cheliped merus lower margin smooth***; major cheliped with distinctively flattened palm, sometimes with strong crest above and below. Pereopod 3 propodus broad, with proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate or subchelate. Female pleopod 2 rami narrower, with more reduced setation than pleopods 3–5; endopod flattened and 2–5 times as long as wide. Pleopods 3–5 with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae reduced and almost embedded in mesial margin of endopod. Uropodal exopod with elevated dorsal plate.

Remarks. Eucalliacidae differ from Callianopsidae, the only other family with a dense field of setae on the distal margin of a truncate maxilliped 3 dactylus, in the propodus of maxilliped 3 being wider than long (rectangular in callianopsids), lacking a lateral longitudinal ridge on the eyestalk (present in callianopsids) and the uropodal exopod having a dorsal plate (absent in callianopsids).

The family and generic concepts used in redefining Eucalliacidae with the support of molecular data, morphological data or both (Robles et al., in press), differ markedly from those tabulated by previous authors including Sakai and Türkay (2014) and Sakai (2018 and his earlier works). Some characters used by previous authors are too variable or not able to be easily categorised for generic diagnosis: anterolateral projections on the carapace, structure of the male pleopod 1, size of appendices internae on pleopods 3–5, relative length of the uropodal endopod, and concavity or convexity of the telson margin. Several of the characters used in this work to separate genera were not considered by these authors.

The family Eucalliacidae has a complex taxonomic history. Manning and Felder (1991) erected the subfamily for two genera, *Eucalliax* and *Calliax*. Ngoc-Ho (2003) erected a new genus *Calliaxina* and differentiated these three genera from *Paraglypturus* Türkay and Sakai, 1995. Sakai (1999a, 2005b) recognised only *Calliax* and *Paraglypturus*, synonymising *Eucalliax* and *Calliaxina* with *Calliax*.

Sakai (2011) divided Eucalliacidae into two subfamilies, Eucalliacinae and Calliapaguropinae, the latter for a single genus, *Calliapagurops* de Saint Laurent, 1973. Sakai's remarks on the new subfamily pointed out differences between *Calliapagurops* and *Callichirus* (a member of another subfamily) but nothing on why the genus was similar to remaining eucalliacids. It is not at all similar. As stated much earlier by Ngoc-Ho (2003), *Calliapagurops* is clearly a member of Callichirinae, here treated as Callichiridae, with which it shares many features. As a result, Sakai's diagnosis of the family comprised only characters true for all or most callianassoids (scaphognathite without long distal seta; pereopod 1 chelate, unequal, dissimilar; uropodal exopod with dorsal plate but without notch) or ambiguous (carapace with or without dorsal oval, maxilliped 3 dactylus "subtriangular" or digitiform). Sakai's (2011) Eucalliacinae revived the genera he had earlier dismissed and added three to bring the total to seven. He re-diagnosed *Calliaxina* using one character alone, not one of those proposed by Ngoc-Ho (2003), but his arguments were not supported by recent molecular or morphological analysis (Robles et al., in press). In this same paper, Sakai corrected his earlier statement (2005) that *Calliax* was the type genus but his reasoning was false. Sakai and Türkay (2014) added an eighth genus and tabulated characters that they believed distinguished them.

Sakai (2018) re-diagnosed Eucalliacinae without emphasising the unifying propodus and dactylus of maxilliped 3. He erected three new genera, *Bakercalliax*, *Heardcalliax* and *Manningcalliax*, here treated as junior synonyms of *Eucalliaxiopsis*. He argued heavily on separation of the genera based on "organs involved in reproduction", especially male pleopods, whether pleopod 1 was "simple" or "subchelate", and on differences in the degree of fusion of the appendices masculina and interna. Pleopod 1 of the male varies considerably and erratically among species of Eucalliacidae

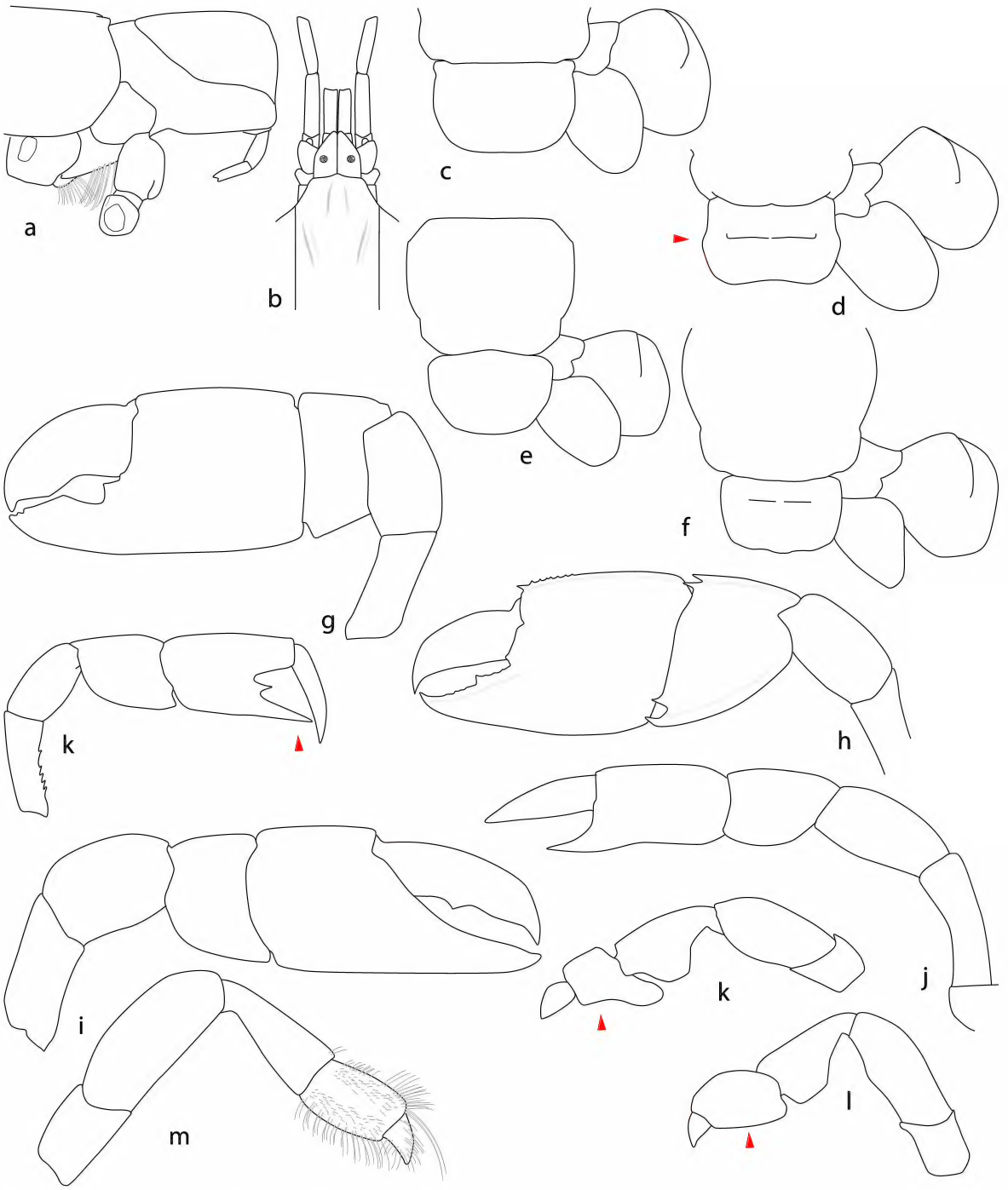

Figure 18. Diagnostic characters for genera of Eucalliacidae. Posterior carapace, sternite 7, pleopod1, coxa 4, basis of pereopod 5: a, *Pseudocalliax*. Carapace, eyestalks, antennules, antennae: b, *Eucalliax*. Telson, uropod: c, *Calliaxina*; d, *Eucalliaxiopsis*. Pleomere 6, telson, uropod: e, *Paraglypturus*; f, *Eucalliax*. Major cheliped: g, *Paraglypturus*; h, *Eucalliax*. Minor cheliped: i, *Paraglypturus*; j, *Calliax*; k, *Pseudocalliax*. Pereopod 3: k, *Calliaxina*; l, *Calliax*. Pereopod 4: m, *Paraglypturus*.

Original illustrations: a, *Pseudocalliax tooradin* NMV J303; e, *Calliaxina* SA-01, UF 36699; h, *Eucalliax quadracuta*, Panama, NHMW 25916.

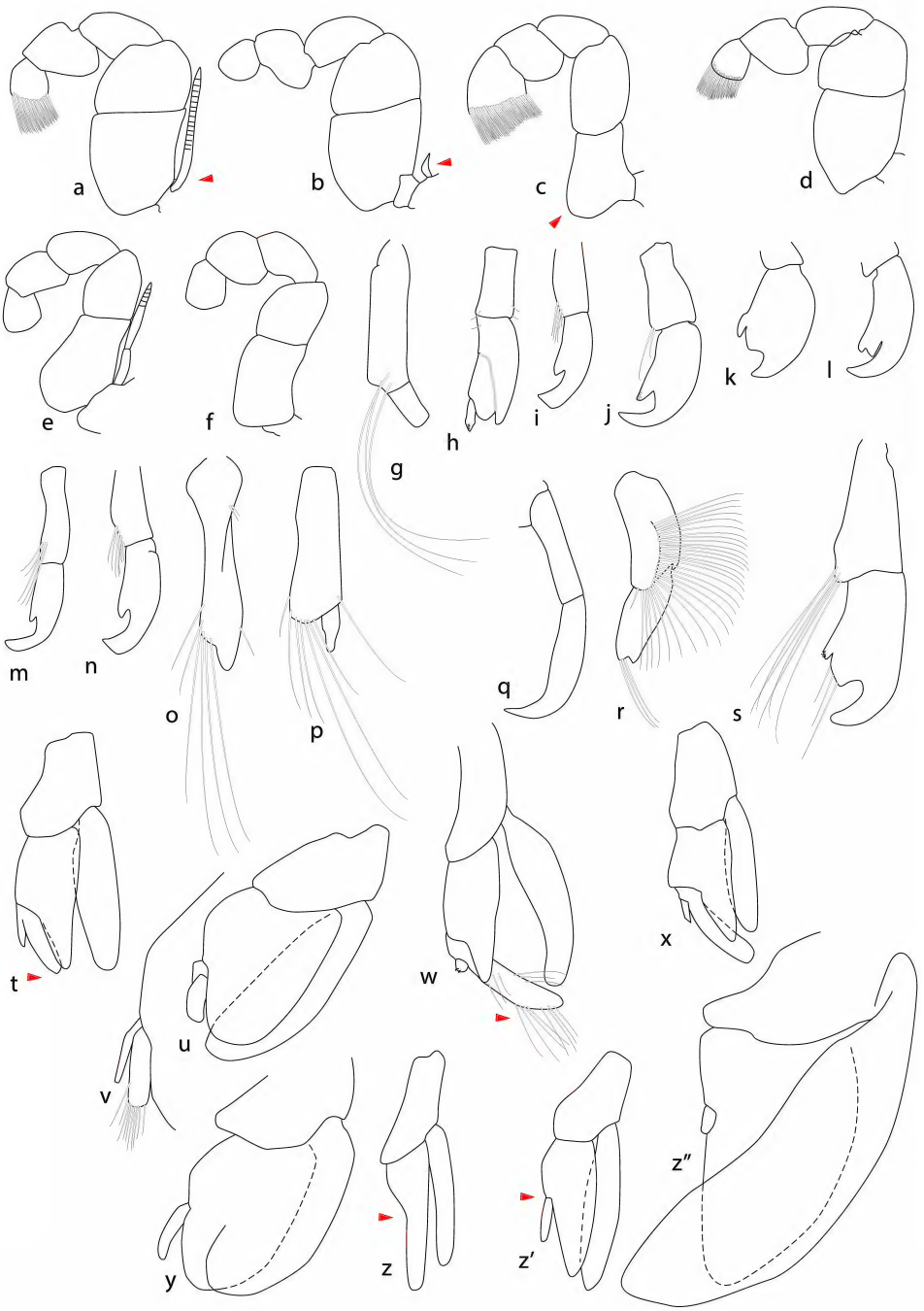

Figure 19. Diagnostic characters for genera of Eucalliacidae. Maxilliped 3: a, *Calliaxina punica*; b, *C.* SA-01; c, *Andamancalliax*; d, *Eucalliaxiopsis*; e, *Pseudocalliax*; f, *Calliax*. Male pleopod 1: g, h, *Calliaxina bulimba*; i, *C. kensleyi*; j, *C.* SA-01; k, *C. punica*; l, *C. sakaii*; m, *Eucalliaxiopsis panglaoensis*; n, *E. mcilhennyi*; o, p, *E. inaequimana*; q, *Calliax*; r, *Pseudocalliax*; s, *Paraglypturus*. Male pleopod 2: t, *Calliaxina*; u, v, *Paraglypturus*; w, *Eucalliax*; x, *Eucalliaxiopsis*. Female pleopod 2, y, *Paraglypturus*: z, *Calliax*; z', *Calliaxina*. Female pleopod 3: z'', *Paraglypturus*.

Original illustrations: b, i, *Calliaxina* SA-01, UF 36699; g, *C. bulimba*, MNHN-IU-2013-7097; h, *C. bulimba*, NMV J71686; w, *Eucalliax quadracuta*, NHMW 25916; o, *Eucalliaxiopsis inaequimana*, MNHN-IU-2013-10008; p, *E. inaequimana*, UF 16512; e, r, *Pseudocalliax tooradin* NMV J303; u, v, *Paraglypturus calderus*, MNHN Th1416.

and appears to have little generic value, contrary to Sakai's (2018) view (figs 19g–s).

Eucalliaxiopsis was differentiated from *Eucalliax* on account of its unusual pleopods 1 and 2. The male pleopod 1 of the type species, *Eucalliax cearaensis*, bears long setae on article 2 (Rodrigues and Manning, 1992), whereas in the type species of *Eucalliax* this article is simple. We were unable to confirm the structure of the male pleopod 1 of *Eucalliax cearaensis* (type mislaid) but Rodrigues and Manning (1992b: fig. 2s) can be variously interpreted. Apart from the long setae, article 2 is similar to that of, for example, *C. jonesi* and *E. panglaoensis* (cf. Dworschak, 2006). In most species of *Calliaxina* and *Eucalliaxiopsis*, the male pleopod 1 has long distal setae on article 1 and a broad article 2 and a curved apex, sometimes with an intermediate lobe. This is seen in *C. novaebritanniae*, *C. kensleyi*, *C. punica*, *C. sakaii*, *E. jonesi*, *E. mcilhennyi* and *E. panglaoensis* (figs 19i–n; see also figures in Dworschak, 2006, 2014; Heard, 1989; Felder and Manning, 1994; Manning and Lemaitre, 1994; Ngoc-Ho, 2003; de Saint Laurent and Manning, 1982). In contrast, the illustrated male pleopod 1 of *C. bulimba* (fig. 19g; Dworschak, 2005: figs 5c, d; Poore and Griffin, 1979: fig. 21g), *E. inaequimana* (fig. 19o, p; Dworschak, 2014: figs 4j–l) and *E. madagassa* (Ngoc-Ho, 2014: fig. 2S, as *C. thomassini*) has article 1 with distal long setae and a short oblique article 2. However, a newly discovered male of *C. bulimba* differs in having a bilobed article 2 with a separate appendix interna (fig. 19h). This would appear to be a precursor of the more typical eucalliacid form (figs 19i–n). A third form of male pleopod 1 is seen in *E. aequimana* where article 2 is longer than article 1, parallel-sided and setose (Dworschak, 2014: figs 9h, i). These forms appear to cross generic lines. The role of ontogeny in the morphology of pleopod 1 is poorly understood but it is evident from some studies that the male pleopod 1 does not appear fully formed in juveniles (Dworschak, 2005, 2006, 2014). Development of the male pleopod 1 with age seems probable.

This throws considerable doubt on the validity of three recently erected genera *Bakercalliax* Sakai, 2018, *Heardcalliax* Sakai, 2018 and *Manningcalliax* Sakai, 2018, all differentiated largely on the basis of the male pleopod 1. Sakai (2018) also noted differences between the relative sizes of the appendices interna and masculina of pleopod 2 but this would scarcely seem of generic value. The type species of all three genera have a transverse ridge on the telson and lack an exopod on maxilliped 3. As a consequence, all are synonymised with *Eucalliaxiopsis*. Sakai (2011) did not compare *Eucalliaxiopsis* with *Calliaxina*, which it resembles more closely, especially in the male pleopod 2. *Calliaxiopsis* Sakai and Türkay, 2014, was synonymised with *Calliaxina* by Poore and Dworschak (2017). Sakai's shuffling of species in his three papers has resulted in some species being listed as members of as many as five genera at different times during their history.

Our morphological analysis (Robles et al., in press) recognised a single clade containing all eleven of the genera included by Sakai (2018) in Eucalliacinae. This monophyly was not supported by the molecular phylogram (Robles et al., in press) where three sequential paraphyletic clades are evident, equivalent to *Eucalliaxiopsis*+*Calliaxina*, *Calliax* and *Eucalliax*.

Key to genera of Eucalliacidae

1. Major chela massive; minor chela with fixed finger acute, shorter than dactylus (fig. 18j); pereopod 3 propodus oval, little longer than wide, with short rounded proximal lobe on lower margin, lower margin straight, upper margin strongly convex (fig. 18l); female pleopod 2 without appendix interna (fig. 19z); scaphocerite small, discoid 2

– Both chelipeds swollen and similar, minor slightly smaller if at all (figs 18g, h); pereopod 3 propodus pentagonal, with strong broadly rounded proximal lobe on lower margin, lower margin concave (fig. 18k); female pleopod 2 with (fig.18z) or without appendix interna; scaphocerite absent or vestigial 3

2. Sternite 7 and pereopod 5 coxa-ischium glabrous; maxilliped 3 ischium linear, exopod absent (fig. 19f); minor cheliped with tooth in gape between fingers (fig. 18k); male pleopod 1 article 2 sickle-shaped (fig. 19q) ..... *Calliax*

– Sternite 7 and pereopod 5 coxa-ischium densely setose (fig. 18a); maxilliped 3 ischium with strong proximal lobe on lower margin, wider proximally than distally, exopod present (fig. 19e); minor cheliped with fixed finger shorter than dactylus (fig. 18j); male pleopod 1 stout, with apical notch (fig. 19r) ..... *Pseudocalliax* (1 species, *P. tooradin*)

3. Uropodal endopod triangular, anterior margin strongly convex, posterior margin straight (fig. 18f); cheliped carpus upper margin with 2 distal sharp spines (fig. 18h); male pleopod 2 appendix masculina 4 times as long as wide, attached near apex of endopod, appendix interna minute (fig. 19w) ..... *Eucalliax* (1 species, *E. quadracuta*)

– Uropodal endopod more or less ovate (figs 18c–e); cheliped carpus upper margin without 2 distal sharp spines; male pleopod 2 appendix masculina longer than wide, attached mesially to endopod with appendix interna, up to twice as long as endopod apex (figs 19t, x) 4

4. Male pleopod 2 appendix masculina a lobe fused with appendix interna, subdistal on endopod margin, endopod broadly triangular (fig. 19u) ..... *Paraglypturus*

– Male pleopod 2 appendix masculina a lobe fused with appendix interna, attached midway on endopod margin, endopod longer than wide (figs 19t, x) 5

5. Telson with transverse ridge, lateral margins convex (fig. 18d) ..... *Eucalliaxiopsis*

– Telson without transverse ridge; lateral margins tapering (fig. 18c) 6

6. Maxilliped 3 ischium and merus length less than twice as long as wide at their articulation, without proximal lobe, with exopod (figs 19a, b) ..... *Calliaxina*

– Maxilliped 3 ischium and merus length twice as long as wide at their articulation; ischium with strong proximal lobe on lower margin, wider proximally than distally (fig. 19c) ..... *Andamancalliax* (1 species, *A. andamanica*)

Implicit attributes. Unless indicated otherwise, the following attributes are implicit throughout the generic diagnoses. Anterior dorsal carapace smooth; cardiac sulci absent. Sternite 7 and pereopod 5, coxa-ischium glabrous. Pleomere 1 without sternal plates. Maxilliped 3 ischium linear or wider distally than proximally. Major cheliped broad, minor cheliped narrower, with long fingers. Major cheliped carpus upper margin apex rounded or square. Minor cheliped fingers closing along length. Male pleopod 2 appendix masculina not reaching tip of endopod. Uropodal endopod ovate, almost symmetrical, anterior margin more convex than posterior margin. Telson smooth dorsally.

Andamancalliax Sakai, 2011

Andamancalliax Sakai, 2011: 494–495.—Sakai, 2018: 738.

Type species. Calliax andamanica Sakai, 2002, by original designation and monotypy.

Diagnosis. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation; ischium with strong proximal lobe on lower margin, wider proximally than distally. ***Major cheliped broad, minor cheliped narrower, with long fingers.*** Male pleopod 1 article 1 with distal long setae, article 2 blade like; without appendix interna. Male pleopod 2 appendix interna digitiform; appendix masculina a lobe fused to appendix interna attached midway on endopod margin. Telson widest anteriorly, more or less semicircular.

Remarks. Andamancalliax was erected for a single species, sharing with species of *Calliaxina* similar pereopod 3, pleopod 3, telson, uropod, and male and female pleopods 2. We have assumed that Sakai's (2002) figure 2B, labelled as from a female, is of the simple male pleopod 1; Sakai (2002) reported it absent but later (Sakai, 2005b, 2011) said it was present, uniramous and with an emarginate tip. It would appear to be a juvenile form. Sakai's (2011) generic diagnosis contains nothing that would distinguish the new genus from any other eucalliacid—in fact it is wrong in stating that the male pleopod 2 lacks an appendix interna—it is clearly figured in Sakai's (2002) mislabelled figure 2A. He provided no justification for the new genus; his key separated *Andamancalliax* with emarginate distal male pleopod 1 article from *Eucalliaxiopsis* where this article was said to incurve distally but the male pleopod 1 of members of the latter varies markedly. *Calliax andamanica* has a more acute rostrum than most species of *Calliaxina* but among its members the rostrum ranges from almost non-existent to sharply triangular (in *C. sakaii*, for example). However, *A. andamanica* has a narrow maxilliped 3 with a proximal lobe (similar to that in *Paraglypturus* spp. and *Pseudocalliax tooradin*) and asymmetrical chelipeds, quite unlike other eucalliacids and the genus is justified. A new species of this genus possesses a small exopod on maxilliped 3, not reported for *A. andamanica* (Poore, in press).

Calliax de Saint Laurent, 1973

Calliax de Saint Laurent, 1973: 514.—Manning, 1987: 397.—Sakai, 1988: 61.—Manning and Felder, 1991: 783.—Sakai, 1999a: 109–110.—Ngoc-Ho, 2003: 489–490.—Sakai, 2005b: 196–197.—Sakai, 2011: 495–496.—Hyžný and Gasparic, 2014: 42–45.—Sakai, 2018: 738.

Type species. Callianassa (*Callichirus*) *lobata* de Gaillande and Lagardère, 1966, by original designation and monotypy.

Diagnosis. Maxilliped 3 ischium and merus narrow, more than twice as long as wide at their articulation. Male major chela with palm about twice as long as carpus, 1.5 times as long as wide, minor chela half as wide, with short fingers. ***Minor cheliped fingers with wide gape, with tooth at base of fingers, fingers not closing along length.*** Male pleopod 1 article 2 curved, simply curving to sharp apex; without appendix interna. Male pleopod 2 appendix interna absent; appendix masculina a lobe fused to appendix interna attached midway on endopod margin, reaching or exceeding tip of endopod. Telson widest anteriorly, more or less semicircular.

Remarks. The wide gape between the fingers of the minor cheliped, with an intermediate tooth, immediately defines species of *Calliax*.

Sakai (1999a) treated *Eucalliax* as a junior synonym of *Calliax* and later (2005b) added *Calliaxina* to this synonymy. Ngoc-Ho (2003) clearly differentiated these three genera and *Paraglypturus*. Sakai (2011) appears to have accepted Ngoc-Ho's arguments and he confined *Calliax* to just two species; one has been added since (Ngoc-Ho, 2014). Sakai's (2011) generic diagnosis contained several generalities referrable to many callianassoids but apart from mention of "P1 unequal in size and dissimilar in shape" acknowledges none of the defining generic characters. His key would fail to discriminate the genus as presently diagnosed. Sakai's (2011) "diagnoses" of the two species are largely replications of his inadequate generic diagnosis, apart from subtle differences in the description of the shapes of their telsons. The type species has been illustrated most recently by Sakai (2017b) and García Raso et al. (2019). Their records are from 622 m and 457–548 m depth respectively in the Mediterranean; previous records are from only a few metres depth.

Calliaxina Ngoc-Ho, 2003

Calliaxina Ngoc-Ho, 2003: 493–494.—Sakai, 2011: 497–498.—Hyžný, 2012: 55–56.—Sakai and Türkay, 2014: 191.—Ngoc-Ho, 2014: 549.—Poore and Dworschak, 2017: 120 (partim).—Sakai, 2018: 739–741.

Calliax.—Sakai, 2005b: 196 (partim, not *Calliax* de Saint Laurent, 1973).

Calliamina Sakai and Türkay, 2014: 190 (misspelling).

Type species. Calliax punica de Saint Laurent and Manning, 1982, by original designation.

Diagnosis. ***Cardiac sulci present.*** Pleomere 1 with pair of sternal plates anterior to pleopods 1. Maxilliped 3 ischium and merus broad, less than twice as long as wide at their articulation. Both chelipeds with palms as long as wide in both sexes, minor slightly smaller if at all. ***Male pleopod 1*** article 1 with distal long setae; article 2 blade-like with bifid apex (sometimes obscure), *or* article 2 much shorter, digitiform (sometimes fused); ***with appendix interna (present at least as hooks on***

endopod). Male pleopod 2 appendix interna digitiform; appendix masculina a lobe fused to appendix interna attached midway on endopod margin. Telson widest anteriorly, more or less semicircular, curving to broad convex apex.

Remarks. Calliaxina differs from *Eucalliaxiopsis* in having a tapering telson without a transverse ridge, and at least a vestige of an appendix interna on pleopod 1 of the male. All species have an exopod on maxilliped 3, sometimes vestigial, whereas only one species of *Eucalliaxiopsis* does.

Calliaxina was erected by Ngoc-Ho (2003) for three species previously included by Sakai (1999a) in *Paraglypturus* Türkay and Sakai, 1995 and later (Sakai, 2005) in *Calliax*. Ngoc-Ho (2003) tabulated differences between these genera but did not include *Eucalliax* Manning and Felder, 1991, which she diagnosed separately in her table. Her diagnosis relied importantly on the presence of an exopod on maxilliped 3, equal and similar chelipeds, appendix interna on pleopods 1 and 2 of the male. Some of her key features are difficult to quantify, notably the shape of the front and anterolateral projections of the carapace, and length of the appendix interna on pleopods 3–5. Sakai (2005) synonymised *Calliaxina* with *Calliax* without discussing any morphological similarities or differences. Later, Sakai (2011) revived *Calliaxina* which he had earlier synonymised in new sense (sensu nov.) by including other species with similar maxillipeds 3 and with one or two cardiac sulci, although some lack maxillipedal 3 exopods. At the same time, he erected a monotypic genus *Eucalliaxiopsis* Sakai, 2011, relying on the possession of unique male pleopods (see below).

As already explained, Robles et al. (in press) divided the species allocated by Sakai (2011) to *Calliaxina* and *Eucalliaxiopsis* into two groups. Their molecular analysis grouped *C. bulimba, C. kensleyi*, *C. novaebritanniae* and *C. sakaii* into a one clade, and *C. aequimana*, *C. inaequimana*, *C. panglaoensis*, *C. jonesi* and three others into a second clade. The morphological treatment includes *C. punica*, type species of *Calliaxina* in the first and *C. cearaensis*, type species of *Eucalliaxiopsis* in the second. These two names are applied to these clades.

Eucalliax Manning and Felder, 1991

Eucalliax Manning and Felder, 1991: 781–783 (partim).—Ngoc-Ho, 2003: 489–490 (partim).—Sakai, 2011: 502–503 (partim).—Hyžný and Hudáčková, 2012: 12–14 (partim).—Sakai, 2017a: 1122 (partim).—Sakai, 2018: 742.

Type species. Callianassa quadracuta Biffar, 1970, by original designation.

Diagnosis. Anterior dorsal carapace with median ridge posterior to rostrum and submedian pair of oblique ridges. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation. Male major cheliped with palm about twice as long as carpus, 1.5 times as long as wide; minor chela slightly smaller, with elongate fingers; ***major cheliped carpus upper margin with 2 distal sharp spines in both sexes***. Male pleopod 1 article 1 with distal long setae; article 2 blade like, with bifid apex, sometimes obscure; without appendix interna. Male pleopod 2 appendix interna minute; appendix masculina 4 times as long as wide, attached near apex of endopod reaching, *or* exceeding tip of endopod. ***Uropodal endopod triangular, anterior margin strongly convex, posterior margin straight***. Telson convex-sided, widest near midpoint, posterior margin slightly excavate; with transverse crest.

Remarks. The most obvious characters distinguishing the only species, *Eucalliax quadracuta*, from other eucalliacids is the triangular uropodal endopod and the male pleopod 2 with its appendix masculina well exceeding the endopod. Re-examination by us (PCD) showed the presence of a minute appendix interna (fig. 19w); Sakai's figure (1999a; fig. 30c) is misleading.

Eucalliax was differentiated initially from *Calliax* simply "in having the chelipeds equal and similar", the two genera being placed in the same new subfamily (Manning and Felder, 1991). The genus was treated as a synonym of *Calliax* by Sakai (1999a, 2005b) without justification but revived later (Sakai, 2011). Sakai (2017a) differentiated *Eucalliax* from *Eucalliaxiopsis* Sakai, 2011 on differences in male pleopods 1 and 2 but not from other genera.

Eucalliaxiopsis Sakai, 2011

Calliaxina.—Ngoc-Ho, 2003: 493–494 (partim).—Sakai, 2011: 497–498 (partim).—Sakai and Türkay, 2014: 191 (partim).—Ngoc-Ho, 2014: 549 (partim).—Poore and Dworschak, 2017: 120 (partim).

Eucalliaxiopsis Sakai, 2011: 503–504.—Sakai, 2018: 742–743.

Calliaxiopsis Sakai and Türkay, 2014: 192.—Sakai, 2018: 741–742 (type species, *Calliaxiopsis madagassa* Sakai and Türkay, 2014, by original designation and monotypy) **syn. nov**.

Bakercalliax Sakai, 2018: 738 (type species, *Callianassa aequimana* Baker, 1907, by original designation) **syn. nov**.

Heardcalliax Sakai, 2018: 743 (type species, *Calliax jonesi* Heard, 1989, by original designation and monotypy) **syn. nov**.

Manningcalliax Sakai, 2018: 743 (type species, *Eucalliax mcilhennyi* Felder and Manning, 1994, by original designation) **syn. nov**.

Type species. Eucalliax cearaensis Rodrigues and Manning, 1992, by original designation and monotypy.

Diagnosis. Anterior dorsal carapace smooth, *or* with median ridge posterior to rostrum and submedian pair of oblique ridges; ***cardiac sulci present***. Pleomere 1 without sternal plates, *or* with pair of sternal plates anterior to pleopods 1. Maxilliped 3 ischium and merus less than twice as long as wide at their articulation. Male major cheliped with palm about twice as long as carpus, 1.5 times as long as wide; minor chela slightly smaller, with elongate fingers or both chelipeds with palms as long as wide in both sexes, minor slightly smaller if at all (rarely). ***Male pleopod 1*** article 2 longer than article 1, parallel-sided, setose, *or* article 1 with distal long setae, article 2 blade like, with bifid apex (sometimes obscure), *or* article 1 with distal long setae, article 2 much shorter, digitiform (sometimes fused); ***without appendix interna***. Male pleopod 2 appendix interna digitiform; appendix masculina a lobe fused to appendix interna attached midway on endopodal margin, reaching or exceeding tip of endopod. Telson convex-sided, widest near midpoint; posterior margin slightly excavate or obscurely excavate between rounded posterolateral corners; ***with transverse crest on dorsal surface***.

Remarks. Eucalliaxiopsis is most easily recognised by the telson having a transverse ridge and convex lateral margins. The male pleopod 1 lacks an appendix interna. The appendix masculina reaches or exceeds the tip of the endopod of pleopod 2. *Eucalliaxiopsis* shares with *Eucalliax* absence of a maxilliped 3 exopod (with one exception, *E. madagassa*) and a telson widest near its midpoint and having a sharp transverse crest. *Eucalliaxiopsis* differs in having an oval rather than rhomboid uropodal endopod. The presence of cardiac sulci is assumed for the type species; it is present in all others illustrated. The generic synonymy is discussed above under the family heading.

Paraglypturus Türkay and Sakai, 1995

Paraglypturus Türkay and Sakai, 1995: 26–27.—Sakai, 1999a: 122.—Sakai, 2005b: 204–205.—Sakai, 2011: 504–505.—Sakai, 2018: 744.

Type species. Paraglypturus calderus Türkay and Sakai, 1995, by original designation and monotypy.

Diagnosis. Maxilliped 3 ischium and merus more than twice as long as wide at their articulation; ischium with strong proximal lobe on lower margin, wider proximally than distally. ***Male major cheliped with palm about twice as long as carpus, 1.5 times as long as wide, minor chela slightly smaller, with elongate fingers.*** Male pleopod 1 article 1 with distal long setae, article 2 blade like, with bifid apex, sometimes obscure; with appendix interna (at least with hooks). Male pleopod 2 appendix interna digitiform; ***appendix masculina a lobe fused with appendix interna, subdistal on endopodal margin.*** Telson widest anteriorly, more or less semicircular.

Remarks. Paraglypturus differs from other Eucalliacidae in having the pleopod 2 endopod almost as wide as that of pleopod 3 (cf. figs 19u, z''). The second article of the pleopod 1 of the male has a minute appendix interna with hooks (fig. 19s). The species share with many eucalliacids two long setae distally on the upper margin of the propodus of pereopod 4 (fig. 18m) but differ in the arrangement of the appendices on the male pleopod 2. The chelipeds are swollen and similar, the minor slightly smaller (figs 18g, i).

Robles et al. (in press) found weak molecular support for one of its two species to be more closely related to Callianopsidae than to any other callianassoids despite the morphological evidence supporting eucalliacid affinities (Sakai (2005b, 2011, 2018). *Paraglypturus* was said by Türkay and Sakai (1995) to be close to *Glypturus* but this was realised to be wrong when Sakai (1999a) noted its similarity to *Calliax* and placed both genera in Eucalliacinae. He differentiated the two on the possession in *Paraglypturus* (in which he included five species) and absence in *Calliax* (seven species) of an exopod on maxilliped 3. Later, Sakai (2005b, 2011) restricted the genus to its type species because it alone possesses the "yellow transparent circular structure on the uropodal endopod". Türkay and Sakai (1995) described and figured a "rounded yellow-transparent circular structure centrally" on the upper surface of the uropodal exopod of *P. calderus*. This was confirmed by PCD on a paratype (SMF 22951) but subsequent examination by GCBP in 2008 and in 2018 of another specimen (MNHN Th1416) failed to distinguish the structure. Ahn et al. (2017) figured in colour a yellow patch on the upper surface of the uropodal *endopod* of *P. tonganus*.

Pseudocalliax Sakai, 2011

Paraglypturus.—Poore, 2004: 184.
Pseudocalliax Sakai, 2011: 505–506.—Sakai, 2018: 744.

Type species. Callianassa tooradin Poore and Griffin, 1979, by original designation and monotypy.

Diagnosis. ***Sternite 7 and pereopod 5 coxa-ischium densely setose.*** Maxilliped 3 ischium and merus more than twice as long as wide at their articulation; ischium with strong proximal lobe on lower margin, wider proximally than distally. Male major cheliped with palm about twice as long as carpus, 1.5 times as long as wide, minor chela half as wide, with short fingers. Minor cheliped fingers with wide gape, without tooth at base of fingers, fingers not closing along length. Male pleopod 1 stout, article 1 setose, article 2 with shallow apical notch; without appendix interna. Male pleopod 2 appendix interna digitiform; appendix masculina not differentiated from endopod apex. Telson widest anteriorly, more or less semicircular.

Remarks. The densely setose sternite 7 and coxa-ischium of pereopod 5 and the stout male pleopod 1 diagnose the only species, *P. tooradin* Poore and Griffin, 1979.

Following "examination of the male specimen [of *C. tooradin*] preserved in the USNM", Sakai (2011) diagnosed *Pseudocalliax* as a genus of Eucalliacidae possessing a dorsal oval and cardiac sulcus but we found no material in the USNM. We have confirmed by examining types and other specimens (NMV J301–J303, J59670–J59672) that the species has neither feature, as was confirmed by Sakai earlier (1999a: figs 33a–c). None of his other generic characters is useful. The male pleopod 1 of *P. tooradin* is not "small and simple" as stated by Sakai (2011) but stout, with article 1 setose and article 2 with shallow apical notch (fig. 19r). The species was inadequately described by Poore and Griffin (1979).

Paracalliacidae Sakai, 2005

Figure 20

Paracalliacinae Sakai, 2005b: 215.
Paracalliacidae.—Dworschak and Poore, 2018: 70.

Diagnosis. Rostrum flat, short, triangular, shorter than eyestalks; ***median carina on rostrum only***; submedian gastric carinae absent; cervical groove well defined; suture between ocular lobe and end of linea thalassinica horizontal in lateral view; anterior branchiostegal margin sinusoidal or semicircular; anterior branchiostegal lobe simple, scarcely calcified, merging smoothly with anterodorsal branchiostegal angle and anterolateral margin of carapace; posterior margin of carapace ***with lateral lobes interacting with anterolateral lobes on pleomere 1.*** Eyestalks flattened, contiguous, with subdistal dorsal cornea. Antennal scaphocerite simple, triangular. Maxilla scaphognathite without long seta on posterior lobe

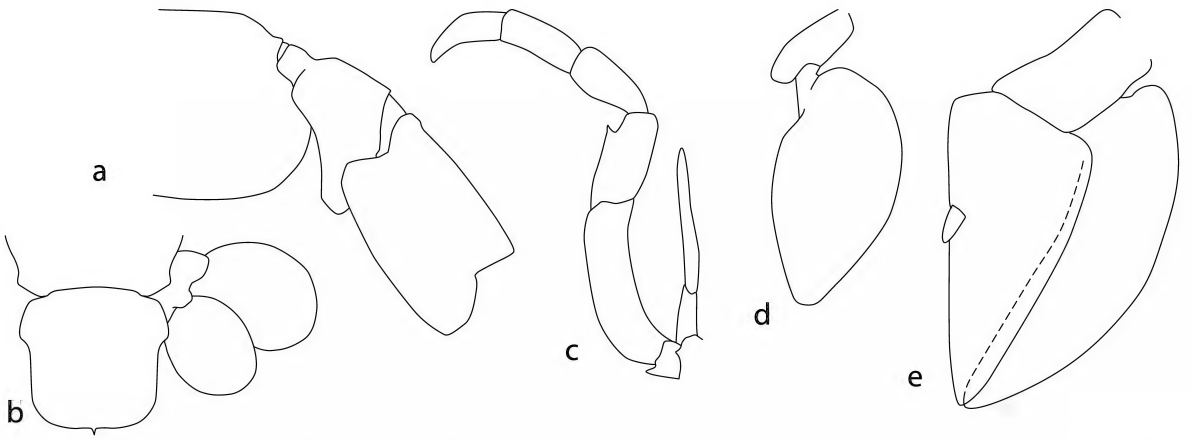

Figure 20. Diagnostic characters for Paracalliacidae, *Paracalliax bollorei*: a, posterior carapace, pleomeres 1, 2; b, telson, uropod; c, maxilliped 3; d, e, female pleopods 1, 2.

extending into branchial chamber. Maxilliped 1 epipod with acute anterior lobe lying alongside exopod. Maxilliped 3 propodus longer than wide, not prominently lobed on lower margin; dactylus slender, digitiform, with setae irregularly spaced along all margins. Cheliped merus lower margin spinose; major cheliped palm oval in cross-section, barely crested above or below. Pereopod 3 propodus elongate-oval, tapering, without proximal lobe on lower margin, without distal spiniform setae on lateral face (often with 1 distal spiniform seta on lower margin). Pereopod 5 minutely chelate or subchelate. Female pleopod 2 rami similar to following pleopods, with regularly setose margins. Pleopods 3–5 with oblique peduncles meeting mesially, endopods triangular, with straight mesial margin, exopods attached laterally, proximally lobed, longer than and enclosing endopods; appendices internae elongate, much longer than wide. Uropodal exopod without elevated dorsal plate.

Remarks. The only species differs from all other callianassoids in having pleomere 1 with dorsolateral lobes interacting and overlapping the posterolateral margin of the carapace (fig. 20a; Dworschak and Poore, 2018; Robles et al., in press). Pleopod 2 is similar to pleopods 3–5 (figs 20d, e). The uropodal exopod lacks a dorsal plate (fig. 20b) and maxilliped 3 is exceptionally narrow (fig. 20c). The male is not known.

Manning and Felder (1991) included the only genus *Paracalliax* in Ctenochelidae. The subfamily was erected as member of Callianassidae by Sakai (2005b) who was uncertain about its affinities (not in Gourretiidae as he asserted later [Sakai, 2011]). The family was ignored by Sakai (2011) and Sakai et al. (2015) who treated the genus as part of Gourretiidae despite treating most other basal groups as distinct families. Sakai (2017a) also included the genus in Gourretiidae but considered it a possible synonym of one of three new gourretiid genera erected at the time.

Paracalliax de Saint Laurent, 1979

Paracalliax de Saint Laurent, 1979a: 1396.—de Saint Laurent and Le Loeuff, 1979: 84–86.—Manning and Felder, 1991: 785.—Sakai, 2005b: 215.—Sakai, 2011: 515.—Sakai et al., 2015: 134.—Sakai, 2017a: 1126, 1131.

Type species. Paracalliax bollorei de Saint Laurent, 1979, by original designation and monotypy.

Diagnosis. With characters of the family.

Remarks. Sakai et al. (2015) described a second species, *Paracalliax stenophthalma*, from the southern Banc d'Arguin, the same locality as the holotype of the type species. They are synonymous (Dworschak and Poore, 2018).

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Table 1. Accepted names of 265 species of callianassoids listed alphabetically by species name, with family allocation and accepted generic and species combination. 87 are in new combinations. Commonly accepted junior synonyms are not included (see WoRMS Editorial Board 2018). Eleven species of Callianassidae inadequately described or figured are placed Incertae sedis. See Table 2 for a list of the same accepted species arranged by family and genus and comments on those Incertae sedis.

Species, Genus	Family allocation	Current combination, authority
abyssa, Lipkecallianassa	Callianassidae	*Lipkecallianassa abyssa* Sakai, 2002
acanthochirus, Glypturus	Callichiridae	*Glypturus acanthochirus* Stimpson, 1866
acanthura, Callianassa	Callianassidae	*Necallianassa acanthura* (Caroli, 1946)
acutirostella, Callianassa	Callianassidae	*Spinicallianassa acutirostella* (Sakai, 1988) **comb. nov.**
adamas, Callianassa	Callichiridae	*Callichirus adamas* (Kensley, 1974)
aequimana, Callianassa (Callichirus)	Eucalliacidae	*Eucalliaxiopsis aequimana* (Baker, 1907) **comb. nov.**
agassizi, Callianassa	Anacalliacidae	*Anacalliax agassizi* (Biffar, 1971)
almeidai, Ctenocheloides	Ctenochelidae	*Ctenocheloides almeidai* Anker & Pachelle, 2013
amboinae, Scallasis	Callianassidae	*Scallasis amboinae* Bate, 1888
amboinensis, Callianassa	Callianassidae	*Rayllianassa amboinensis* (De Man, 1888)
amplimaxilla, Callianassa	Callianassidae	*Aqaballianassa amplimaxilla* (Sakai, 2002) **comb. nov.**
andamanica, Calliax	Eucalliacidae	*Andamancalliax andamanica* (Sakai, 2002)
andamaniensis, Trypaea	Callianassidae	*Scallasis andamaniensis* (Sakai, 2010) **comb. nov.**
angelikae, Neocallichirus	Callichiridae	*Neocallichirus angelikae* Sakai, 2000
anoploura, Callianassa	Callianassidae	Incertae sedis *anoploura* Sakai, 2002
anovalis, Callianopsis	Callianopsidae	*Callianopsis anovalis* Lin, Komai & Chan, 2007
aqabaensis, Callianassa	Callianassidae	*Aqaballianassa aqabaensis* (Dworschak, 2003) **comb. nov.**
arenosa, Callianassa	Callianassidae	*Arenallianassa arenosa* (Poore, 1975) **comb. nov.**
argentinensis, Callianassa	Anacalliacidae	*Anacalliax argentinensis* (Biffar, 1971)
arguinensis, Gilvossius	Callianassidae	*Gilvossius arguinensis* Sakai, Türkay, Beuck & Freiwald, 2015
armata, Callianassa	Callichiridae	*Glypturus armatus* (A.Milne-Edwards, 1870)
articulata, Callianassa	Callichiridae	*Corallianassa articulata* (Rathbun, 1906)
arutyunovi, Vulcanocalliax	Callianopsidae	*Vulcanocalliax arutyunovi* Dworschak & Cunha, 2007
assimilis, Callianassa (Callichirus)	Callichiridae	*Corallianassa assimilis* (De Man, 1928)
attenboroughi, Ctenocheloides	Ctenochelidae	*Ctenocheloides attenboroughi* Anker, 2010
auchenorhynchus, Neocallichirus	Callichiridae	*Neocallichirus auchenorhynchus* Sakai, 2005
audax, Callianassa	Callichiridae	*Audacallichirus audax* (De Man, 1911) **comb. nov.**
aungtonyae, Gourretia	Ctenochelidae	*Paragourretia aungtonyae* (Sakai, 2002)
australiensis, Trypaea	Callianassidae	*Trypaea australiensis* Dana, 1852
australis, subterranea, Callianassa	Callianassidae	*Callianassa australis* Kensley, 1974
Balssi, Callianassa (Callichirus)	Callichiridae	*Balsscallichirus balssi* (Monod, 1933)
balssi, Ctenocheles	Ctenochelidae	*Ctenocheles balssi* Kishinouye, 1926
bangensis, Callianassa	Callianassidae	*Rayllianassa bangensis* (Sakai, 2005) **comb. nov.**
barracuda, Gourretia	Ctenochelidae	*Gourretia barracuda* LeLoeuff & Intès, 1974
berylae, Necallianassa	Callianassidae	*Necallianassa berylae* Heard & Manning, 1998
bicauda, Notiax	Callianassidae	*Pugnatrypaea bicauda* (Sakai, 2010) **comb. nov.**
biffari, Callianassa	Callianassidae	*Neotrypaea biffari* (Holthuis, 1991)
biffari, Gourretia	Ctenochelidae	*Paragourretia biffari* (Blanco-Rambla & Liñero-Arana, 1994)
biformis, Callianassa	Callianassidae	*Biffarius biformis* (Biffar, 1971)
bocourti, Callianassa	Callichiridae	*Lepidophthalmus bocourti* (A. Milne-Edwards, 1870)
bollorei, Paracalliax	Paracalliacidae	*Paracalliax bollorei* de Saint Laurent, 1979
borradailei, longiventris, Callianassa	Callichiridae	*Corallianassa borradailei* (De Man, 1928)
boucheti, Ctenocheloides	Ctenochelidae	*Ctenocheloides boucheti* Poore, 2015
Bouvieri, Callianassa	Callianassidae	*Paratrypaea bouvieri* (Nobili, 1904)
brachyophthalma, Callianassa	Callianassidae	*Notiax brachyophthalma* (A.Milne-Edwards, 1870)
brachytelson, Callianassa	Callianassidae	*Cheramoides brachytelson* (Sakai, 2002) **comb. nov.**
brevirostris, Callianassa	Callianassidae	*Aqaballianassa brevirostris* (Sakai, 2002) **comb. nov.**

Species, Genus	Family allocation	Current combination, authority
bulimba, Callianassa	Eucalliacidae	*Calliaxina bulimba* (Poore & Griffin, 1979)
cacahuate, Neocallichirus	Callichiridae	*Neocallichirus cacahuate* Felder & Manning, 1995
caechabitator, Neocallichirus	Callichiridae	*Neocallichirus caechabitator* Sakai, 1988
caecigena, Callianassa	Callianopsidae	*Callianopsis caecigena* (Alcock & Anderson, 1894)
caesari, Pseudobiffarius	Callianassidae	*Neotrypaea ca*esari (Heard & Manning, 2000) **comb. nov.**
calderus, Paraglypturus	Eucalliacidae	*Paraglypturus calderus* Türkay & Sakai, 1995
caledonica, Callianassa	Callianassidae	*Scallasis caledonica* (Ngoc-Ho, 1991) **comb. nov.**
californiensis, Callianassa	Callianassidae	*Neotrypaea californiensis* (Dana, 1854)
Calmani, Callianassa	Callichiridae	*Neocallichirus calmani* (Nobili, 1904)
candidus, Cancer	Callianassidae	*Gilvossius candidus* (Olivi, 1792)
cavifrons, Cheramus	Callianassidae	*Caviallianassa cavifrons* (Komai & Fujiwara, 2012) **comb. nov.**
cearaensis, Eucalliax	Eucalliacidae	*Eucalliaxiopsis cearaensis* (Rodrigues & Manning, 1992)
ceramica, Callianassa	Callianassidae	*Filhollianassa ceramica* (Fulton & Grant, 1906) **comb. nov.**
chakratongae, Callianassa	Callianassidae	Incertae sedis *chakratongae* Sakai, 2002
charcoti, Calliapagurops	Callichiridae	*Calliapagurops charcoti* de Saint Laurent, 1973
collaroy, Callianassa	Callichiridae	*Corallianassa collaroy* (Poore & Griffin, 1979)
collini, Ctenocheles	Ctenochelidae	*Ctenocheles collini* Ward, 1945
contipes, Callianassa	Callianassidae	*Scallasis contipes* (Sakai, 2002) **comb. nov.**
convexa, Callianassa	Callianassidae	*Gilvossius convexus* (de Saint Laurent & LeLoeuff, 1979)
coolibah, Gourretia	Ctenochelidae	*Paragourretia coolibah* (Poore & Griffin, 1979)
coriolisae, Callianassa	Callianassidae	*Coriollianassa coriolisae* (Ngoc-Ho, 2014) **comb. nov.**
costaricensis, Callianassa	Callianassidae	*Neotrypaea costaricensis* (Sakai, 2005) **comb. nov.**
Coutierei, Callianassa	Callichiridae	*Corallianassa coutierei* (Nobili, 1904)
crosnieri, Gourretia	Ctenochelidae	*Paragourretia crosnieri* (Ngoc-Ho, 1991)
darwinensis, Neocallichirus	Callichiridae	*Neocallichirus darwinensis* Sakai, 1988
darvishi, Neocallichirus	Callichiridae	*Neocallichirus darvishi* Sepahvand, Komai, Momtazi & Shahabi, 2018
debilis, Biffarius	Callianassidae	*Fragillianassa debilis* (Hernandez-Aguilera, 1998) **comb. nov.**
delicatulus, Biffarius	Callianassidae	*Biffarius delicatulus* Rodrigues & Manning, 1992
denticulata, Callianassa	Ctenochelidae	*Gourretia denticulata* (Lutze, 1937)
diaphora, Callianassa	Callianassidae	*Callianassa diaphora* LeLoeuff & Intes, 1974
doerjesti, Calliax	Eucalliacidae	*Calliax doerjesti* Sakai, 1999
ehsani, Callianassa	Callianassidae	*Aqaballianassa ehsani* (Sepahvand, Tudge & Momtazi, 2018) **comb. nov.**
Eiseni, Lepidophthalmus	Callichiridae	*Lepidophthalmus eiseni* Holmes, 1904
exilimaxilla, Callianassa	Callianassidae	Incertae sedis *exilimaxilla* Sakai, 2005
filholi, Callianassa	Callianassidae	*Filhollianassa filholi* (A.Milne-Edwards, 1878) **comb. nov.**
foresti, Callichirus	Callichiridae	*Balsscallichirus foresti* (LeLoeuff & Intès, 1974) **comb. nov.**
foresti, Calliapagurops	Callichiridae	*Calliapagurops foresti* Ngoc-Ho, 2002
fragilis, Callianassa	Callianassidae	*Fragillianassa fragilis* (Biffar, 1970) **comb. nov.**
frouini, Neocallichirus	Callichiridae	*Neocallichirus frouini* Ngoc-Ho, 2005
galathea, Tuerkaygourretia	Ctenochelidae	*Paragourretia galathea* (Sakai, 2017) **comb. nov.**
garthi, Callianassa	Callichiridae	*Callichirus garthi* (Retamal, 1975)
gaucho, Poti	Callianassidae	*Poti gaucho* Rodrigues & Manning, 1992
geomar, Bathycalliax	Callianopsidae	*Bathycalliax geomar* Sakai & Türkay, 1999
gigas, Callianassa	Callianassidae	*Neotrypaea gigas* (Dana, 1852)
gilchristi, Callianassa	Callichiridae	*Balsscallichirus gilchristi* (Barnard, 1947)
goniophthalma, Callianassa	Callianopsidae	*Callianopsis goniophthalma* (Rathbun, 1902)
grandidieri, Callianassa	Callichiridae	*Lepidophthalmus grandidieri* (Coutière, 1899)
grandimana, Callianassa	Callichiridae	*Neocallichirus grandimana* (Gibbes, 1850)
grandis, Neocallichirus	Callichiridae	*Laticallichirus grandis* (Karasawa & Goda, 1996)
gruneri, Callianassa	Callianassidae	Incertae sedis *gruneri* Sakai, 1999
guaiqueri, Sergio	Callichiridae	*Neocallichirus guaiqueri* (Blanco-Rambla, Liñero-Arana & Beltràn Lares, 1995)

Species, Genus	Family allocation	Current combination, authority
guara, Callianassa	Callichiridae	*Neocallichirus guara* (Rodrigues, 1971)
guassutinga, Callianassa	Callichiridae	*Neocallichirus guassutinga* (Rodrigues, 1971)
guineensis, Callianassa	Callichiridae	*Balsscallichirus guineensis* (De Man, 1928)
hainanensis, Nihonotrypaea	Callianassidae	*Neotrypaea hainanensis* (Liu & Liu, 2014) **comb. nov.**
harmandi, Callianassa	Callianassidae	*Neotrypaea harmandi* (Bouvier, 1901) **comb. nov.**
hartmeyeri, Callianassa	Callichiridae	*Corallianassa hartmeyeri* (Schmitt, 1935)
haswelli, Callianassa	Callichiridae	*Corallianassa haswelli* (Poore & Griffin, 1979)
holthuisi, Ctenocheles	Ctenochelidae	*Ctenocheles holthuisi* Rodrigues, 1978
horneri, Neocallichirus	Callichiridae	*Neocallichirus horneri* Sakai, 1988
inaequimana, Eucalliax	Eucalliacidae	*Eucalliaxiopsis inaequimana* (Dworschak, 2014) **comb. nov.**
indica, Michaelcallianassa	Callichiridae	*Michaelcallianassa indica* Sakai, 2002
intermedia, Callianassa	Callianassidae	*Pugnatrypaea intermedia* (De Man, 1905) **comb. nov.**
intesi, Callichirus	Callichiridae	*Corallianassa intesi* (de Saint Laurent & LeLoeuff, 1979)
iranicus, Cheramus	Callianassidae	*Pugnatrypaea iranica* (Sepahvand, Momtazi & Tudge, 2015) **comb. nov.**
islagrande, Callianassa	Callichiridae	*Callichirus islagrande* (Schmitt, 1935)
jamaicense, Callianassa	Callichiridae	*Lepidophthalmus jamaicense* (Schmitt, 1935)
japonica, subterranea, Callianassa	Callianassidae	*Neotrypaea japonica* (Ortmann, 1891) **comb. nov.**
joculatrix, Callianassa	Callianassidae	*Jocullianassa joculatrix* (De Man, 1905) **comb. nov.**
jonesi, Calliax	Eucalliacidae	*Eucalliaxiopsis jonesi* (Heard, 1989) **comb. nov.**
Jousseaumei, Callianassa	Callichiridae	*Neocallichirus jousseaumei* (Nobili, 1904)
karumba, Callianassa	Callichiridae	*Karumballichirus karumba* (Poore & Griffin, 1979) **comb. nov.**
kensleyi, Eucalliax	Eucalliacidae	*Calliaxina kensleyi* (Dworschak, 2005)
kowalevski, Trypaea	Callianassidae	*Jocullianassa kowalevski* (Sakai, 2010) **comb. nov.**
kraussi, Callianassa	Callichiridae	*Kraussillichirus kraussi* (Stebbing, 1900) **comb. nov.**
laevidactyla, Gourretia	Ctenochelidae	*Paragourretia laevidactyla* (Liu & Liu, 2010) **comb. nov.**
lahouensis, Gourretia	Ctenochelidae	*Paragourretia lahouensis* (LeLoeuff & Intes, 1974)
lanceolata, Callianassa (Callichirus)	Callichiridae	*Corallianassa lanceolata* (Edmondson, 1944)
laresi, Gourretia	Ctenochelidae	*Gourretia laresi* Blanco-Rambla & Liñero-Arana, 1994
latispina, Callianassa	Ctenochelidae	*Dawsonius latispina* (Dawson, 1967)
laurae, Callichirus	Callichiridae	*Glypturus laurae* (de Saint Laurent, 1984)
loeuffintesi, Gourretia	Ctenochelidae	*Gourretia loeuffintesi* Sakai, 2011
lemaitrei, Neocallichirus	Callichiridae	*Neocallichirus lemaitrei* Manning, 1993
leviceps, Ctenocheles	Ctenochelidae	*Ctenocheles leviceps* Rabalais, 1979
lewtonae, Callianassa	Callianassidae	*Aqaballianassa lewtonae* (Ngoc-Ho, 1994) **comb. nov.**
lignicola, Callianassa	Callianassidae	*Raylianassa lignicola* (Alcock & Anderson, 1899) **comb. nov.**
limosa, Callianassa	Callianassidae	*Biffarius limosus* (Poore, 1975)
lobata, Callianassa	Eucalliacidae	*Calliax lobata* (de Gaillande & Lagardere, 1966)
lobetobensis, Callianassa	Callianassidae	*Pugnatrypaea lobetobensis* (De Man, 1905) **comb. nov.**
longicauda, Callianassa	Callianassidae	*Praedatrypaea longicauda* (Sakai, 1967) **comb. nov.**
longiventris, Callianassa	Callichiridae	*Corallianassa longiventris* (A.Milne-Edwards, 1870)
louisianensis, jamaicense, Callianassa	Callichiridae	*Lepidophthalmus louisianensis* (Schmitt, 1935)
madagassa, Calliaxiopsis	Eucalliacidae	*Eucalliaxiopsis madagassa* (Sakai & Türkay, 2014) **comb. nov.**
madagassa, Callianassa	Callichiridae	*Lepidophthalmus madagassus* (Lenz & Richters, 1881) **comb. nov.**
major, Callianassa	Callichiridae	*Callichirus major* (Say, 1818)
makarovi, Nihonotrypaea	Callianassidae	*Neotrypaea makarovi* (Marin, 2013) **comb. nov.**
malaccaensis, Callianassa	Callianassidae	*Coriollianassa malaccaensis* (Sakai, 2002) **comb. nov.**
maldivensis, Callianassa	Callianassidae	*Paratrypaea maldivensis* (Borradaile, 1904)
manihinae, Gourretia	Ctenochelidae	*Gourretia manihinae* Sakai, 1984
manningi, Lepidophthalmus	Callichiridae	*Lepidophthalmus manningi* Felder & Staton, 2000
manningi, Neocallichirus	Callichiridae	*Neocallichirus manningi* Kazmi & Kazmi, 1992
maorianus, Ctenocheles	Ctenochelidae	*Ctenocheles maorianus* Powell, 1949

Species, Genus	Family allocation	Current combination, authority
marchali, Callianassa	Callianassidae	*Callianassa marchali* LeLoeuff & Intes, 1974
marginata, Callianassa	Callianassidae	*Cheramoides marginata* (Rathbun, 1901)
martensi, Callianassa	Callichiridae	*Corallianassa martensi* (Miers, 1884)
maryae, Neocallichirus	Callichiridae	*Neocallichirus maryae* Karasawa, 2004
masoomi, Callianassa	Callichiridae	*Balsscallichirus masoomi* (Tirmizi, 1970)
matzi, Callianassa	Callianassidae	*Jocullianassa matzi* (Sakai, 2002) **comb. nov.**
mauritana, Phaetoncalliax	Callianopsidae	*Callianopsis mauritana* (Sakai, Türkay, Beuck & Freiwald, 2015)
mauritiana, Callianassa	Callichiridae	*Neocallichirus mauritianus* (Miers, 1882)
mcilhennyi, Eucalliax	Eucalliacidae	*Eucalliaxiopsis mcilhennyi* (Felder & Manning, 1994) **comb. nov.**
melissae, Biffarius	Callianassidae	*Neotrypaea melissae* (Poore, 2008) **comb. nov.**
mericeae, Sergio	Callichiridae	*Neocallichirus mericeae* (Manning & Felder, 1995) **comb. nov.**
mirim, Callianassa	Callichiridae	*Audacallichirus mirim* (Rodrigues, 1971) **comb. nov.**
mocambiquensis, Callianassa	Callichiridae	*Mocallichirus mocambiquensis* (Sakai, 2004) **comb. nov.**
modesta, Callianassa (Calliactites)	Callianassidae	*Praedatrypaea modesta* (De Man, 1905) **comb. nov.**
moluccensis, Callianassa (Cheramus)	Callichiridae	*Neocallichirus moluccensis* (De Man, 1905)
monodi, Callichirus	Callichiridae	*Audacallichirus monodi* (de Saint Laurent & LeLoeuff, 1979) **comb. nov.**
mortenseni, Neocallichirus	Callichiridae	*Neocallichirus mortenseni* Sakai, 2005
mucronata, Callianassa	Callichiridae	*Mucrollichirus mucronatus* (Strahl, 1862) **comb. nov.**
natalensis, Callianassa	Callichiridae	*Neocallichirus natalensis* (Barnard, 1947)
natesi, Lepidophthalmus	Callichiridae	*Lepidophthalmus natesi* Felder & Robles, 2015
ngochoae, Callianassa	Callianassidae	Incertae sedis *ngochoae* Sakai, 1999
nickellae, Neocallichirus	Callichiridae	*Neocallichirus nickellae* Manning, 1993
nieli, Callianassa	Callianassidae	*Aqaballianassa nieli* (Sakai, 2002) **comb. nov.**
nigroculata, Callianassa	Callianassidae	Incertae sedis *nigroculata* Sakai, 200
nomurai, Ctenocheloides	Ctenochelidae	*Kiictenochelodes nomurai* (Komai, 2013)
nosybeensis, Gourretia	Ctenochelidae	*Gourretia nosybeensis* Sakai, 2004
novae-britanniae, Callianassa	Eucalliacidae	*Calliaxina novaebritanniae* (Borradaile, 1900) **comb. nov.**
oblonga, Callianassa	Callianassidae	*Cheramoides oblonga* (LeLoeuff & Intes, 1974) **comb. nov.**
ohuranus, Cheramus	Callianassidae	*Spinicallianassa ohurana* (Komai, Maenosono & Fujita, 2014) **comb. nov.**
orientalis, Cheramus	Callianassidae	*Pugnatrypaea orientalis* (Bate, 1888) **comb. nov.**
pachydactyla, Callianassa	Callichiridae	*Neocallichirus pachydactyla* (A. Milne-Edwards, 1870)
pacificus, Biffarius	Callianassidae	*Neotrypaea pacifica* (Guzmán &Thatje, 2003) **comb. nov.**
panamensis, Lepidophthalmus	Callichiridae	*Lepidophthalmus panamensis* Felder & Robles, 2015
panglaoensis, Eucalliax	Eucalliacidae	*Eucalliaxiopsis panglaoensis* (Dworschak, 2006) **comb. nov.**
parva, Callianassa (Calliactites)	Callianassidae	*Rayllianassa parva* (Edmondson, 1944) **comb. nov.**
parvula, Callianassa	Callianassidae	*Spinicallianassa parvula* (Sakai, 1988) **comb. nov.**
pentagonocephala, Callianassa	Callichiridae	*Audacallichirus pentagonocephala* (Rossignol, 1962) **comb. nov.**
persica, Callianassa	Callianassidae	*Callianassa persica* Sakai, 2005
petalura, Callianassa	Callianassidae	*Neotrypaea petalura* (Stimpson, 1860) **comb. nov.**
phuketensis, Gourretia	Ctenochelidae	*Paragourretia phuketensis* (Sakai, 2002)
pixii, Callianassa	Callichiridae	*Balsscallichirus pixii* (Kensley, 1976) **comb. nov.**
plantei, Callianassa	Callianassidae	Incertae sedis *plantei* Sakai, 2004
plantei, Thaumastochelopsis	Ctenochelidae	*Ctenocheles plantei* (Burukovsky, 2005)
pola, Neocallichirus	Callichiridae	*Neocallichirus pola* Sakai & Türkay, 2014
poorei, Callianassa	Callianassidae	*Tastrypaea poorei* (Sakai, 1999) **comb. nov.**
portsudanensis, Pseudogourretia	Ctenochelidae	*Paragourretia portsudanensis* (Sakai, 2005) **comb. nov.**
praedatrix, Callianassa	Callianassidae	*Praedatrypaea praedatrix* (De Man, 1905) **comb. nov.**
profunda, Callianassa	Callianassidae	*Cheramus profundus* (Biffar, 1973)
propinqua, Callianassa	Callianassidae	*Praedatrypaea propinqua* (De Man, 1905) **comb. nov.**
propriopedis, Callianassa	Callianassidae	Incertae sedis *propriopedis* Sakai, 2002
pugnatrix, Callianassa	Callianassidae	*Pugnatrypaea pugnatrix* (De Man, 1905) **comb. nov.**

Species, Genus	Family allocation	Current combination, authority
punica, Calliax	Eucalliacidae	*Calliaxina punica* (de Saint Laurent & Manning, 1982)
pygmaea, Callianassa	Callianassidae	*Scallasis pygmaea* (De Man, 1928) **comb. nov.**
qeshmensis, Gourretia	Ctenochelidae	*Gourretia qeshmensis* Sepahvand, Pouyani & Momtazi, 2016
quadracuta, Callianassa	Eucalliacidae	*Eucalliax quadracuta* (Biffar, 1970)
rabalaisae, Glypturus	Callichiridae	*Glypturus rabalaisae* Sakai, 2011
rafai, Lepidophthalmus	Callichiridae	*Lepidophthalmus rafai* Felder & Manning, 1998
ranongensis, Callianassa (*Callichirus*)	Callichiridae	*Thailandcallichirus ranongensis* (Sakai, 1983)
raymanningi, Neocallichirus	Callichiridae	*Neocallichirus raymanningi* Blanco-Rambla & Lemaitre, 1999
rhopalommata, Laurentgourretia	Ctenochelidae	*Laurentgourretia rhopalommata* Sakai, 2004
richardi, Lepidophthalmus	Callichiridae	*Lepidophthalmus richardi* Felder & Manning, 1997
Rochei, Callianassa	Callianassidae	*Neotrypaea rochei* (Bouvier, 1895)
Rosae, Callianassa (Callichirus)	Callichiridae	*Lepidophthalmus rosae* (Nobili, 1904)
rotundicaudata, Callianassa	Callianassidae	*Gilvossius rotundicaudatus* (Stebbing, 1902)
rotundocula, Trypaea	Callianassidae	Incertae sedis *rotundocula* Sakai & Türkay, 2014
rudisulcus, Raylianassa	Callianassidae	*Rudisullianassa rudisulcus* (Komai, Fujita & Maenosono, 2014) **comb. nov.**
sahul, Callianassa	Callianassidae	*Raylianassa sahul* (Poore, 2008) **comb. nov.**
sakaii, Calliax	Eucalliacidae	*Calliaxina sakaii* (de Saint Laurent, 1979)
santarita, Notiax	Callianassidae	*Notiax santarita* Thatje, 2000
santarosaensis, Callichirus	Callichiridae	*Callichirus santarosaensis* Sakai & Türkay, 2012
sassandrensis, Callichirus	Callichiridae	*Neocallichirus sassandrensis* (LeLoeuff & Intès, 1974)
seilacheri, Callianassa	Callichiridae	*Callichirus seilacheri* (Bott, 1955)
serrifrons, Ctenocheles	Ctenochelidae	*Ctenocheles serrifrons* LeLoeuff & Intès, 1974
setimanus, Gonodactylus	Callianassidae	*Gilvossius setimanus* (DeKay, 1844)
Sibogae, Callianassa	Callianassidae	*Coriollianassa sibogae* (De Man, 1905) **comb. nov.**
sinica, Michaelcallianassa	Callichiridae	*Michaelcallianassa sinica* Liu & Liu, 2009
sinica, Gourretia	Ctenochelidae	*Gourretia sinica* Liu & Liu, 2010
sinuensis, Lepidophthalmus	Callichiridae	*Lepidophthalmus sinuensis* Lemaitre & Rodrigues, 1991
siriboia, Lepidophthalmus	Callichiridae	*Lepidophthalmus siriboia* Felder & Rodrigues, 1993
spinicauda, Cheramus	Callianassidae	*Spinicallianassa spinicauda* (Komai, Maenosono & Fujita, 2014) **comb. nov.**
spinoculata, Callianassa	Callianassidae	*Aqaballianassa spinoculata* (Sakai, 2005) **comb. nov.**
spinophthalma, Callianassa	Callianassidae	*Scallasis spinophthalma* (Sakai, 1970) **comb. nov.**
spinorostra, Trypaea	Callianassidae	*Jocullianassa spinorostra* (Sakai, 2010) **comb. nov.**
spiridonovi, Callichiropsis	Callichiridae	*Neocallichirus spiridonovi* (Sakai, 2010) **comb. nov.**
statoni, Lepidophthalmus	Callichiridae	*Lepidophthalmus statoni* Felder, 2015
stenomastaxa, Callianassa	Callianassidae	Incertae sedis *stenomastaxa* Sakai, 2002
subterraneus, Cancer (Astacus)	Callianassidae	*Callianassa subterranea* (Montagu, 1808)
sulfureus, Sergio	Callichiridae	*Neocallichirus sulfureus* (Lemaitre & Felder, 1996)
tabogensis, Callianassa	Callianassidae	*Neotrypaea tabogensis* (Sakai, 2005)
tamakii, Grynaminna	Callichiridae	*Grynaminna tamakii* Poore, 2000
tenuimanus, Callichirus	Callichiridae	*Balsscallichirus tenuimanus* (de Saint Laurent & LeLoeuff, 1979)
tenuipes, Callianassa	Callianassidae	Incertae sedis *tenuipes* Sakai, 2002
thailandica, Callianassa	Callianassidae	*Caviallianassa thailandica* (Sakai, 2005) **comb. nov.**
thalesapensis, Neocallichirus	Callichiridae	*Karumballichirus thalesapensis* (Sakai & Lheknim, 2014) **comb. nov.**
thermophila, Nihonotrypaea	Callianassidae	*Neotrypaea thermophila* (Lin, Komai & Chan, 2007) **comb. nov.**
thorsoni, Callianassa	Callianassidae	*Aqaballianassa thorsoni* (Sakai, 2005) **comb. nov.**
timiris, Neocallichirus	Callianassidae	*Callianassa timiris* (Sakai, Türkay, Beuck & Freiwald, 2015) **comb. nov.**
tonganus, Paraglypturus	Eucalliacidae	*Paraglypturus tonganus* Ahn, Kim, Ju & Min, 2017
tonkinae, Callianassa (Scallasis)	Callianassidae	*Scallasis tonkinae* (Grebenjuk, 1975) **comb. nov.**
tooradin, Callianassa	Eucalliacidae	*Pseudocalliax tooradin* (Poore & Griffin, 1979)
tridentata, Callianassa	Callichiridae	*Lepidophthalmus tridentatus* (von Martens, 1868)
trilobata, Callianassa	Callichiridae	*Glypturoides trilobata* (Biffar, 1970)

Species, Genus	Family allocation	Current combination, authority
truncata, Callianassa	Callianassidae	*Necallianassa truncata* (Giard & Bonnier, 1890)
tulearensis, Calliax	Eucalliacidae	*Calliax tulearensis* Ngoc-Ho, 2014
turnerana, Callianassa	Callichiridae	*Lepidophthalmus turneranus* (White, 1861)
tyrrhenus, Astacus	Callianassidae	*Gilvossius tyrrhenus* (Petagna, 1792)
uncinata, Callianassa	Callianassidae	*Neotrypaea uncinata* (H.Milne Edwards, 1837)
variabilis, Callianassa (Cheramus)	Callichiridae	*Neocallichirus variabilis* (Edmondson, 1944)
vaugelasi, Neocallichirus	Callichiridae	*Neocallichirus vaugelasi* Dworschak, 2011
vietnamensis, Trypaea	Callianassidae	*Jocullianassa vietnamensis* (Sakai, 2010) **comb. nov.**
vigilax, Callianassa (Callichirus)	Callichiridae	*Neocallichirus vigilax* (De Man, 1916)
whitei, Callianassa	Callianassidae	*Gilvossius whitei* (Sakai, 1999)
winslowi, Callianassa (Callichirus)	Callichiridae	*Corallianassa winslowi* (Edmondson, 1944)
xishaensis, Calliaxina	Eucalliacidae	*Calliaxina xishaensis* Liu & Liang, 2016
xutha, Corallianassa	Callichiridae	*Corallianassa xutha* Manning, 1988
zarenkovi, Paragourretia	Ctenochelidae	*Gourretia zarenkovi* (Sakai, 2010) **comb. nov.**

Table 2. Accepted names of 265 species of callianassoids listed alphabetically by family and genus. 87 are in new combinations. Commonly accepted junior synonyms are not included (see WoRMS Editorial Board 2018). Eleven species of Callianassidae inadequately described or figured are placed incertae sedis at the end of the table.

Anacalliacidae
Anacalliax agassizi (Biffar, 1971)
Anacalliax argentinensis (Biffar, 1971)

Callianassidae
Aqaballianassa amplimaxilla (Sakai, 2002) **comb. nov.**
Aqaballianassa aqabaensis (Dworschak, 2003) **comb. nov.**
Aqaballianassa brevirostris (Sakai, 2002) **comb. nov.**
Aqaballianassa ehsani (Sepahvand, Tudge & Momtazi, 2018) **comb. nov.**
Aqaballianassa lewtonae (Ngoc-Ho, 1994) **comb. nov.**
Aqaballianassa nieli (Sakai, 2002) **comb. nov.**
Aqaballianassa spinoculata (Sakai, 2005) **comb. nov.**
Aqaballianassa thorsoni (Sakai, 2005) **comb. nov.**
Arenallianassa arenosa (Poore, 1975) **comb. nov.**
Biffarius biformis (Biffar, 1971)
Biffarius delicatulus Rodrigues & Manning, 1992
Biffarius limosus (Poore, 1975)
Callianassa australis Kensley, 1974
Callianassa diaphora LeLoeuff & Intès, 1974
Callianassa marchali LeLoeuff & Intès, 1974
Callianassa persica Sakai, 2005
Callianassa subterranea (Montagu, 1808)
Callianassa timiris (Sakai, Türkay, Beuck & Freiwald, 2015) **comb. nov.**
Caviallianassa cavifrons (Komai & Fujiwara, 2012) **comb. nov.**
Caviallianassa thailandica (Sakai, 2005) **comb. nov.**
Cheramoides brachytelson (Sakai, 2002) **comb. nov.**
Cheramoides marginata (Rathbun, 1901)
Cheramoides oblonga (LeLoeuff & Intes, 1974) **comb. nov.**
Cheramus profundus (Biffar, 1973)
Coriollianassa coriolisae (Ngoc-Ho, 2014) **comb. nov.**
Coriollianassa malaccaensis (Sakai, 2002) **comb. nov.**
Coriollianassa sibogae (De Man, 1905) **comb. nov.**
Filhollianassa ceramica (Fulton & Grant, 1906) **comb. nov.**
Filhollianassa filholi (A.Milne-Edwards, 1878) **comb. nov.**
Fragillianassa debilis (Hernandez-Aguilera, 1998) **comb. nov.**
Fragillianassa fragilis (Biffar, 1970) **comb. nov.**
Gilvossius arguinensis Sakai, Türkay, Beuck & Freiwald, 2015
Gilvossius candidus (Olivi, 1792)
Gilvossius convexus (de Saint Laurent & LeLoeuff, 1979)
Gilvossius rotundicaudatus (Stebbing, 1902)
Gilvossius setimanus (DeKay, 1844)
Gilvossius tyrrhenus (Petagna, 1792)
Gilvossius whitei (Sakai, 1999)
Jocullianassa joculatrix (De Man, 1905) **comb. nov.**
Jocullianassa matzi (Sakai, 2002) **comb. nov.**
Jocullianassa spinorostra (Sakai, 2010) **comb. nov.**
Jocullianassa vietnamensis (Sakai, 2010) **comb. nov.**
Jocullianassa kowalevski (Sakai, 2010) **comb. nov.**
Lipkecallianassa abyssa Sakai, 2002
Necallianassa acanthura (Caroli, 1946)
Necallianassa berylae Heard & Manning, 1998
Necallianassa truncata (Giard & Bonnier, 1890)
Neotrypaea biffari (Holthuis, 1991)
Neotrypaea caesari (Heard & Manning, 2000) **comb. nov.**
Neotrypaea californiensis (Dana, 1854)

Neotrypaea costaricensis (Sakai, 2005) **comb. nov.**
Neotrypaea gigas (Dana, 1852)
Neotrypaea hainanensis (Liu & Liu, 2014) **comb. nov.**
Neotrypaea harmandi (Bouvier, 1901) **comb. nov.**
Neotrypaea japonica (Ortmann, 1891) **comb. nov.**
Neotrypaea makarovi (Marin, 2013) **comb. nov.**
Neotrypaea melissae (Poore, 2008) **comb. nov.**
Neotrypaea pacifica (Guzmán &Thatje, 2003) **comb. nov.**
Neotrypaea petalura (Stimpson, 1860) **comb. nov.**
Neotrypaea rochei (Bouvier, 1895)
Neotrypaea tabogensis (Sakai, 2005)
Neotrypaea thermophila (Lin, Komai & Chan, 2007) **comb. nov.**
Neotrypaea uncinata (H.Milne Edwards, 1837)
Notiax brachyophthalma (A.Milne-Edwards, 1870)
Notiax santarita Thatje, 2000
Paratrypaea bouvieri (Nobili, 1904)
Paratrypaea maldivensis (Borradaile, 1904)
Poti gaucho Rodrigues & Manning, 1992
Praedatrypaea longicauda (Sakai, 1967) **comb. nov.**
Praedatrypaea modesta (De Man, 1905) **comb. nov.**
Praedatrypaea praedatrix (De Man, 1905) **comb. nov.**
Praedatrypaea propinqua (De Man, 1905) **comb. nov.**
Pugnatrypaea bicauda (Sakai, 2010) **comb. nov.**
Pugnatrypaea intermedia (De Man, 1905) **comb. nov.**
Pugnatrypaea iranica (Sepahvand, Momtazi & Tudge, 2015) **comb. nov.**
Pugnatrypaea lobetobensis (De Man, 1905) **comb. nov.**
Pugnatrypaea orientalis (Bate, 1888) **comb. nov.**
Pugnatrypaea pugnatrix (De Man, 1905) **comb. nov.**
Raylianassa amboinensis (De Man, 1888)
Raylianassa bangensis (Sakai, 2005) **comb. nov.**
Raylianassa lignicola (Alcock & Anderson, 1899) **comb. nov.**
Raylianassa parva (Edmondson, 1944) **comb. nov.**
Raylianassa sahul (Poore, 2008) **comb. nov.**
Rudisullianassa rudisulcus (Komai, Fujita & Maenosono, 2014) **comb. nov.**
Scallasis amboinae Bate, 1888
Scallasis andamaniensis (Sakai, 2010) **comb. nov.**
Scallasis caledonica (Ngoc-Ho, 1991) **comb. nov.**
Scallasis contipes (Sakai, 2002) **comb. nov.**
Scallasis pygmaea (De Man, 1928) **comb. nov.**
Scallasis spinophthalma (Sakai, 1970) **comb. nov.**
Scallasis tonkinae (Grebenjuk, 1975) **comb. nov.**
Spinicallianassa acutirostella (Sakai, 1988) **comb. nov.**
Spinicallianassa ohurana (Komai, Maenosono & Fujita, 2014) **comb. nov.**
Spinicallianassa parvula (Sakai, 1988) **comb. nov.**
Spinicallianassa spinicauda (Komai, Maenosono & Fujita, 2014) **comb. nov.**
Tastrypaea poorei (Sakai, 1999) **comb. nov.**
Trypaea australiensis Dana, 1852

Callianopsidae
Bathycalliax geomar Sakai & Türkay, 1999
Callianopsis anovalis Lin, Komai & Chan, 2007
Callianopsis caecigena (Alcock & Anderson, 1894)
Callianopsis goniophthalma (Rathbun, 1902)
Callianopsis mauritana (Sakai, Türkay, Beuck & Freiwald, 2015)
Vulcanocalliax arutyunovi Dworschak & Cunha, 2007

Callichiridae
Audacallichirus audax (De Man, 1911) **comb. nov.**
Audacallichirus mirim (Rodrigues, 1971) **comb. nov.**

Audacallichirus monodi (de Saint Laurent & LeLoeuff, 1979) **comb. nov.**
Audacallichirus pentagonocephala (Rossignol, 1962) **comb. nov.**
Balsscallichirus balssi (Monod, 1933)
Balsscallichirus foresti (LeLoeuff & Intes, 1974) **comb. nov.**
Balsscallichirus gilchristi (Barnard, 1947)
Balsscallichirus guineensis (De Man, 1928)
Balsscallichirus masoomi (Tirmizi, 1970)
Balsscallichirus pixii (Kensley, 1976) **comb. nov.**
Balsscallichirus tenuimanus (de Saint Laurent & LeLoeuff, 1979)
Calliapagurops charcoti de Saint Laurent, 1973
Calliapagurops foresti Ngoc-Ho, 2002
Callichirus adamas (Kensley, 1974)
Callichirus garthi (Retamal, 1975)
Callichirus islagrande (Schmitt, 1935)
Callichirus major (Say, 1818)
Callichirus santarosaensis Sakai & Türkay, 2012
Callichirus seilacheri (Bott, 1955)
Corallianassa articulata (Rathbun, 1906)
Corallianassa assimilis (De Man, 1928)
Corallianassa borradailei (De Man, 1928)
Corallianassa collaroy (Poore & Griffin, 1979)
Corallianassa coutierei (Nobili, 1904)
Corallianassa hartmeyeri (Schmitt, 1935)
Corallianassa haswelli (Poore & Griffin, 1979)
Corallianassa intesi (de Saint Laurent & LeLoeuff, 1979)
Corallianassa lanceolata (Edmondson, 1944)
Corallianassa longiventris (A.Milne-Edwards, 1870)
Corallianassa martensi (Miers, 1884)
Corallianassa winslowi (Edmondson, 1944)
Corallianassa xutha Manning, 1988
Glypturoides trilobata (Biffar, 1970)
Glypturus acanthochirus Stimpson, 1866
Glypturus armatus (A.Milne-Edwards, 1870)
Glypturus laurae (de Saint Laurent, 1984)
Glypturus rabalaisae Sakai, 2011
Grynaminna tamakii Poore, 2000
Karumballichirus karumba (Poore & Griffin, 1979) **comb. nov.**
Karumballichirus thalesapensis (Sakai & Lheknim, 2014) **comb. nov.**
Kraussillichirus kraussi (Stebbing, 1900) **comb. nov.**
Laticallichirus grandis (Karasawa & Goda, 1996)
Lepidophthalmus bocourti (A. Milne-Edwards, 1870)
Lepidophthalmus eiseni Holmes, 1904
Lepidophthalmus grandidieri (Coutière, 1899)
Lepidophthalmus jamaicense (Schmitt, 1935)
Lepidophthalmus louisianensis (Schmitt, 1935)
Lepidophthalmus madagassus (Lenz & Richters, 1881) **comb. nov.**
Lepidophthalmus manningi Felder & Staton, 2000
Lepidophthalmus natesi Felder & Robles, 2015
Lepidophthalmus panamensis Felder & Robles, 2015
Lepidophthalmus rafai Felder & Manning, 1998
Lepidophthalmus richardi Felder & Manning, 1997
Lepidophthalmus rosae (Nobili, 1904)
Lepidophthalmus sinuensis Lemaitre & Rodrigues, 1991
Lepidophthalmus siriboia Felder & Rodrigues, 1993
Lepidophthalmus statoni Felder, 2015
Lepidophthalmus tridentatus (von Martens, 1868)
Lepidophthalmus turneranus (White, 1861)
Michaelcallianassa indica Sakai, 2002

Michaelcallianassa sinica Liu & Liu, 2009
Mocallichirus mocambiquensis (Sakai, 2004) **comb. nov.**
Mucrollichirus mucronatus (Strahl, 1862) **comb. nov.**
Neocallichirus angelikae Sakai, 2000
Neocallichirus auchenorhynchus Sakai, 2005
Neocallichirus cacahuate Felder & Manning, 1995
Neocallichirus caechabitator Sakai, 1988
Neocallichirus calmani (Nobili, 1904)
Neocallichirus darwinensis Sakai, 1988
Neocallichirus darvishi Sepahvand, Komai, Momtazi & Shahabi, 2018
Neocallichirus frouini Ngoc-Ho, 2005
Neocallichirus grandimana (Gibbes, 1850)
Neocallichirus guaiqueri (Blanco-Rambla, Liñero-Arana & Beltràn Lares, 1995)
Neocallichirus guara (Rodrigues, 1971)
Neocallichirus guassutinga (Rodrigues, 1971)
Neocallichirus horneri Sakai, 1988
Neocallichirus jousseaumei (Nobili, 1904)
Neocallichirus lemaitrei Manning, 1993
Neocallichirus manningi Kazmi & Kazmi, 1992
Neocallichirus maryae Karasawa, 2004
Neocallichirus mauritianus (Miers, 1882)
Neocallichirus mericeae (Manning & Felder, 1995) **comb. nov.**
Neocallichirus moluccensis (De Man, 1905)
Neocallichirus mortenseni Sakai, 2005
Neocallichirus natalensis (Barnard, 1947)
Neocallichirus nickellae Manning, 1993
Neocallichirus pachydactyla (A. Milne-Edwards, 1870)
Neocallichirus pola Sakai & Türkay, 2014
Neocallichirus raymanningi Blanco-Rambla & Lemaitre, 1999
Neocallichirus sassandrensis (LeLoeuff & Intes, 1974)
Neocallichirus spiridonovi (Sakai, 2010) **comb. nov.**
Neocallichirus sulfureus (Lemaitre & Felder, 1996)
Neocallichirus variabilis (Edmondson, 1944)
Neocallichirus vaugelasi Dworschak, 2011
Neocallichirus vigilax (De Man, 1916)
Thailandcallichirus ranongensis (Sakai, 1983)

Ctenochelidae
Ctenocheles balssi Kishinouye, 1926
Ctenocheles collini Ward, 1945
Ctenocheles holthuisi Rodrigues, 1978
Ctenocheles leviceps Rabalais, 1979
Ctenocheles maorianus Powell, 1949
Ctenocheles plantei (Burukovsky, 2005)
Ctenocheles serrifrons LeLoeuff & Intes, 1974
Ctenocheloides almeidai Anker & Pachelle, 2013
Ctenocheloides attenboroughi Anker, 2010
Ctenocheloides boucheti Poore, 2015)
Dawsonius latispina (Dawson, 1967)
Gourretia barracuda LeLoeuff & Intes, 1974
Gourretia denticulata (Lutze, 1937)
Gourretia laresi Blanco-Rambla & Linero-Arana, 1994
Gourretia loeuffintesi Sakai, 2011
Gourretia manihinae Sakai, 1984
Gourretia nosybeensis Sakai, 2004
Gourretia qeshmensis Sepahvand, Pouyani & Momtazi, 2016
Gourretia sinica Liu & Liu, 2010
Gourretia zarenkovi (Sakai, 2010) **comb. nov.**

Kiictenochelodes nomurai (Komai, 2013)
Laurentgourretia rhopalommata Sakai, 2004
Paragourretia aungtonyae (Sakai, 2002)
Paragourretia biffari (Blanco-Rambla & Liñero-Arana, 1994)
Paragourretia coolibah (Poore & Griffin, 1979)
Paragourretia crosnieri (Ngoc-Ho, 1991)
Paragourretia galathea (Sakai, 2017) **comb. nov.**
Paragourretia laevidactyla (Liu & Liu, 2010) **comb. nov.**
Paragourretia lahouensis (LeLoeuff & Intès, 1974)
Paragourretia phuketensis (Sakai, 2002)
Paragourretia portsudanensis (Sakai, 2005) **comb. nov.**

Eucalliacidae
Andamancalliax andamanica (Sakai, 2002)
Calliax doerjesti Sakai, 1999
Calliax lobata (de Gaillande & Lagardère, 1966)
Calliax tulearensis Ngoc-Ho, 2014
Calliaxina bulimba (Poore & Griffin, 1979)
Calliaxina kensleyi (Dworschak, 2005)
Calliaxina novaebritanniae (Borradaile, 1900) **comb. nov.**
Calliaxina punica (de Saint Laurent & Manning, 1982)
Calliaxina sakaii (de Saint Laurent, 1979)
Calliaxina xishaensis Liu & Liang, 2016
Eucalliax quadracuta (Biffar, 1970)
Eucalliaxiopsis aequimana (Baker, 1907) **comb. nov.**
Eucalliaxiopsis cearaensis (Rodrigues & Manning, 1992)
Eucalliaxiopsis inaequimana (Dworschak, 2014) **comb. nov.**
Eucalliaxiopsis jonesi (Heard, 1989) **comb. nov.**
Eucalliaxiopsis madagassa (Sakai & Türkay, 2014) **comb. nov.**
Eucalliaxiopsis mcilhennyi (Felder & Manning, 1994) **comb. nov.**
Eucalliaxiopsis panglaoensis (Dworschak, 2006) **comb. nov.**
Paraglypturus calderus Türkay & Sakai, 1995
Paraglypturus tonganus Ahn, Kim, Ju & Min, 2017
Pseudocalliax tooradin (Poore & Griffin, 1979)

Paracalliacidae
Paracalliax bollorei de Saint Laurent, 1979

Callianassidae incertae sedis
Callianassa tenuipes Sakai, 2002 – few illustrations, possibly *Jocullianassa*
Callianassa anoploura Sakai, 2002 – few illustrations
Callianassa chakratongae Sakai, 2002 – female only described
Callianassa exilimaxilla Sakai, 2005 – female only illustrated, possibly *Jocullianassa*
Callianassa gruneri Sakai, 1999 – few illustrations
Callianassa nigroculata Sakai, 2002 – female only illustrated, possibly *Scallasis*
Callianassa ngochoae Sakai, 1999 – female only described
Callianassa plantei Sakai, 2004 – possibly two species in illustrated material; chelipeds from holotype typical of *Paratrypaea* but maxilliped 3 from another specimen of narrow form
Callianassa propriopedis Sakai, 2002 – female only described
Callianassa stenomastaxa Sakai, 2002 – female only described (possibly same species as *C. propriopedis*)
Trypaea rotundocula Sakai & Türkay, 2014 – female only described